A QUALITATIVE AND QUANTITATIVE INVESTIGATION OF THE BEHAVIOUR OF THE LONGHORN SCULPIN, **MYOXOCEPHALUS OCTODECEMSPINOSUS** (MITCHILL 1815), WITH SPECIAL REFERENCE TO FEEDING

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A QUALITATIVE AND QUANTITATIVE INVESTIGATION OF THE BEHAVIOUR OF THE LONGHORN SCULPIN, *Myoxocephalus octodecemspinosus* (Mitchill 1815), WITH SPECIAL REFERENCE TO FEEDING.

by

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ABSTRACT

Behavioural observations of Myoxocephalus octodecemspinosus were made by diving at two locations on the Avalon Peninsula. Qualitative descriptions of the daily activity were compiled with two fundamental postures, REST and ALERT, and four behaviours, rooting, agonism, locomotion, and feeding, being observed. A behavioural profile for the longhorn sculpin was derived from these descriptions.

Feeding behaviour occurs in a stereotyped pattern, similar in its basic form to the feeding of other marine and freshwater predators. Despite these behavioural characteristics, the longhorn is an ineffective predator of smaller benthic fish species. Field observations indicated that the longhorn is primarily a visual feeder. Laboratory experiments however, revealed that this species also employs other sensory modes for the detection of food.

Stomach contents, intestinal contents, and occurrence of digestive stages in specimens caught over a 24 hour period, indicated cyclic feeding during the capelin (Mallotus villosus), spawning period. However, an Analysis of Variance (MANOVA), revealed that time was not the most important factor affecting ingestion.

Caloric analysis of selected prey organisms indicated that

capelin, with a value of 5341 calories per gram dry weight, is the most energy rich food resource for inshore populations of the longhorn sculpin. Large scale movements of M. octodecemspinosus to shallower, inshore waters of Newfoundland during the early summer are suggested to be a phenomenon related to the availability of this food resource.

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INTRODUCTION

The longhorn sculpin, Myoxocephalus octodecemspinosus (Mitchill 1815), is an abundant benthic fish of the North Atlantic coastal waters of Canada and the United States. Morrow (1951) provides most of the known information on this species in a detailed account of its taxonomic history and biology. Distribution records and morphological descriptions are given by Bigelow and Schroeder (1953) and Leim and Scott (1966).

Fritz (1965), Kohler et al. (1970), Scott (1971), and Tyler (1971a) describe seasonal changes in the relative abundance and distribution of offshore longhorn populations and give information on the length-weight relationships of this species. The most recent published data on this sculpin are Tyler's (1971b, 1972) seasonal analysis of stomach contents. Studies of shallow water inshore populations are lacking however, and there are no published descriptions of the longhorn sculpin's behaviour.

LeDrew (1972) found a significant proportion of the diet of M. aeneus (grubby) was juvenile radiated shannies (Ulvaria subbifurcata), and states that this shanny may be vulnerable to predation because of its diurnal activity pattern. Longhorn sculpins are voracious feeders and may also be efficient predators of smaller benthic fish like the radiated shanny or the rock gunnel (Pholis gunnelus). This study is a qualitative and quantitative investigation of the behaviour of M. octodecemspinosus undertaken to determine its significance as a benthic

predator and to provide a foundation for further studies of its behavioural ecology.

MATERIALS AND METHODS

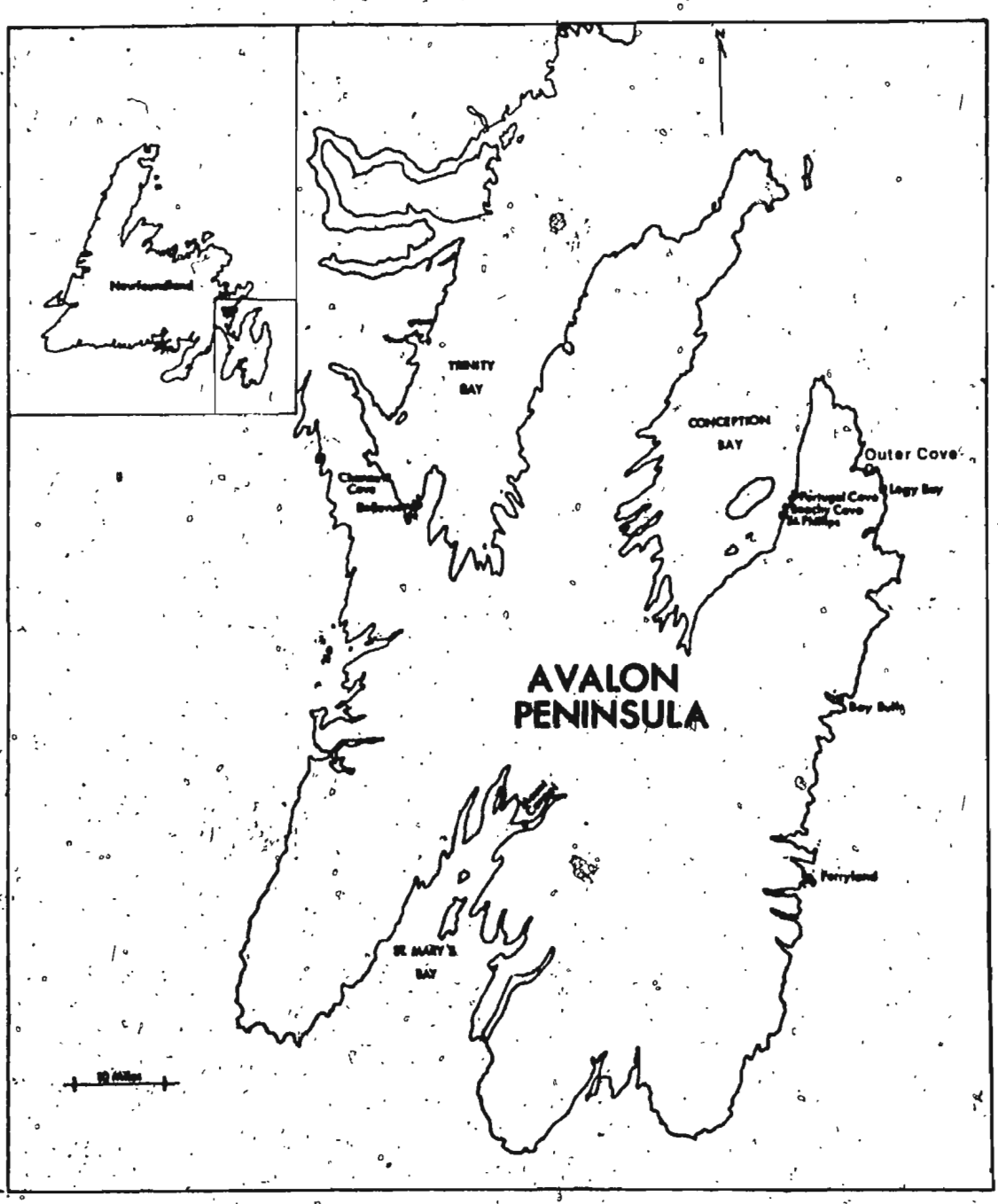
I. FIELD WORK

(i) Ethological Studies

Two sites were chosen for direct observations of longhorn behaviour during the summer of 1973, (see Figure 1). At Outer Cove, longhorns were abundant inshore at shallow depths (2 - 7 metres) and underwater visibility was excellent on most occasions, (approx. 12 - 20 metres). A mask, fins, and snorkel were used to observe the fish from the surface of the water. St. Phillips, the second site, had much poorer visibility underwater (approx. 3 - 7 metres), and longhorns were not common in the shallow inshore waters. Scuba was used to observe sculpins at depths ranging from 5 - 15 metres. Observing fish from behind blinds did not eliminate the effect of exhaust bubbles on natural behaviour. By remaining approximately 3 metres above the substrate, it was possible to make prolonged observations of the sculpins with no apparent disturbance of their behaviour.

Each observation was a 35 - 45 minute continuous period during which postural details and associated changes, movements, and specific motor patterns were recorded on a slate. For each period, the observer swam offshore on the surface and began observations when the first

Figure 1. The Avalon Peninsula, showing two diving sites where Myoxocephalus octodecemspinosus was collected and observed.


Newfoundland
TRINITY BAY
CONCEPTION BAY
Outer Cove
Logy Bay
AVALON PENINSULA
Bay Bulls
Ferryland
ST. MARY'S BAY

motionless longhorn sculpin was encountered. Since the natural occurrence of feeding behaviour in the field was so low, a number of methods were used to induce sculpin feeding. At St. Phillips, scuba divers made direct observations of sculpin responses to individual rock gunnels and radiated shannies trapped in 4.5 litre glass jars placed on the bottom. Feeding responses to shannies trapped in plastic bags filled with seawater and to white, neutrally buoyant styrofoam floats were also observed at this location. A Bolex 16 mm movie camera was used to record the feeding attacks on the trapped shanny and on the float, and this film was analyzed in the laboratory.

An underwater habitat at St. Phillips, LORA I, enabled observations to be made in relative comfort and safety. Thawed capelin (Mallotus villosus) were released from the entry hatch of the habitat and longhorn feeding responses to large aggregates of cunner (Tautogolabrus adspersus) attracted by this bait were documented. Floodlights on the exterior of LORA I also attracted cunner and observations could be made at dusk. Poor underwater visibility and the restricted fields of view from the domed portholes of LORA I limited the value of some observations. Feeding activity and associated postures of the sculpins were observed through the entry hatch of the habitat.

At Outer Cove, live rock gunnels were released in the water column above aggregates of longhorns and sculpin predatory behaviour was observed. Responses to gunnels set in minnow traps placed on the substrate, and to

baited and unbaited lines lowered from the surface were also observed. These established feeding situations at both locations made possible a more complete description of longhorn feeding behaviour.

The swimming behaviour of the longhorn was also quantified during each observation interval. Periods of continuous swimming (excursions), and the number of direction changes during each excursion (turns), were recorded for the entire observation interval. These two actions were distinct, recognizeable patterns and were quantified as reliable measures of the longhorn's swimming activity.

All observations were made during daylight; sunrise to noon observations were designated A.M. and noon to sunset observations were designated P.M. Quantitative observations were made on longhorns at Outer Cove (7 individuals in A.M. and 8 in P.M. for a total of 630 minutes of observations), and at St. Phillips (3 individuals in A.M. and 6 in P.M. for a total of 320 minutes of observations).

During each observation interval, 3 specific behaviours (feeding, agonism, and rooting) and 1 Modal Action Pattern (stalk) were enumerated providing a second quantitative measure of the longhorn sculpin's behaviour in the natural habitat.

An experiment was performed at St. Phillips to determine the functional significance of the observed locomotor behaviour (i.e. the excursion/turn activity). During August 1973, 8 longhorns were hand netted by scuba divers, tagged, and placed in a large nylon netted

steel frame cage for a starvation period of 7 to 14 days. The cage was elevated 4 feet from the substrate on an iron platform to ensure that no feeding occurred. After the starvation period, these experimental sculpins were released individually and their swimming behaviour observed and quantified using the technique previously described.

At St. Phillips, the movements of both the experimental and the non-experimental fish were recorded onto a slate during each observation period. Although these maps were not to scale, they did indicate general direction changes and relative distances from known underwater landmarks.

(ii) Feeding Periodicity Study

The standard procedure of sampling stomach contents over a 24 hour period (Darnell, 1958), was employed to determine the diel nature of the sculpin's feeding behaviour. Longhorn sculpins were abundant at Outer Cove, a shallow, pebble/rock bottom bay with large sand patches, and so this site was chosen for the 24 hour sampling. In July 1973, starting at 1600 hours, 6 sculpins were hand netted by scuba divers every four hours throughout the following 24 hour period. After each dive, live weights and total lengths of each specimen were measured. The live fish were then killed by placement in a concentrated solution of the anaesthetic MS 222. Entire stomachs and attached intestinal tracts were removed and immediately preserved in 90 % ethanol. Within 24 hours of

collection, the samples were frozen, then during the following few weeks, individually thawed and analyzed. The preserved samples were frozen because of the extended time period between sampling and analysis of the contents. This prevented deterioration of the samples before analysis. Stomach contents were identified, weighed wet, and the relative stage of digestion noted. Decomposition of capelin based on previous laboratory digestion studies revealed three characteristic stages: STAGE I ... capelin intact, body firm, with some evidence of exterior deterioration; STAGE II ... vertebrae revealed with small pieces of firm muscle attached, head and tail missing except for the skeletal remains; and STAGE III ... soft mash of pulpy muscle, vertebrae and anterior skeleton only. As the 24 hour diving was conducted during the capelin spawning period, this fish species was the primary component of the sculpin's diet and thus, relative digestion stages were easy to determine. Intestinal contents were stripped and weighed wet. The wet samples were then oven dried at 80 °C. for approximately two weeks to a constant weight. Dry weights of the stomach and intestinal contents were expressed as a ratio to the wet weight of the fish, i.e. grams dry weight of contents per kilogram wet weight of fish. With this technique, three different quantified measures (stomach contents, intestinal contents, and frequency of occurrence of the three digestive stages), could be used to assess the feeding pattern over the diel period.

II. LABORATORY WORK

(i) Light/Dark Feeding Study

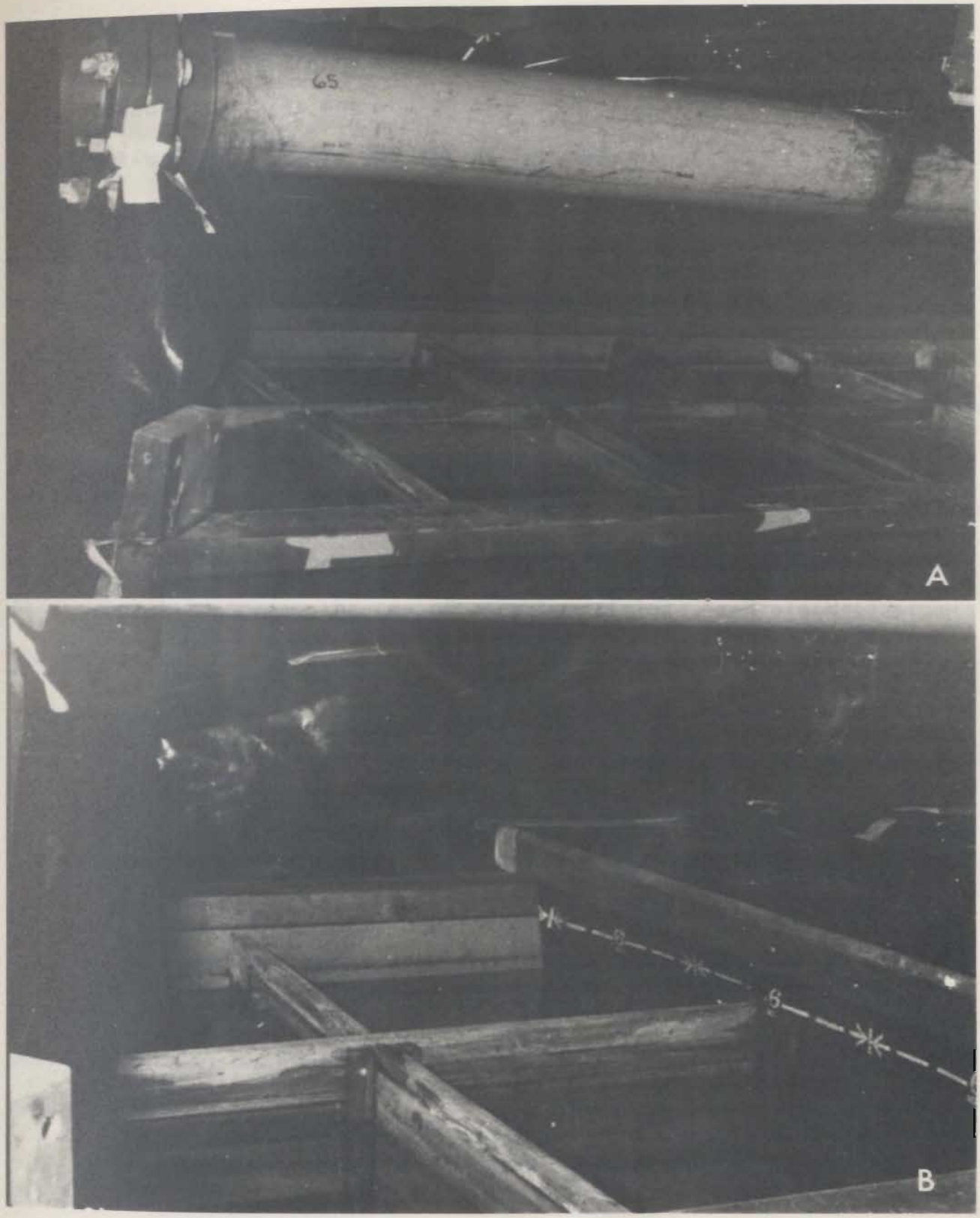
A replicated series of laboratory experiments were performed to determine the effects of light and time of day on the feeding success of the longhorn sculpin. In May 1973, scuba divers hand netted 40 sculpins from Middle Cove, Newfoundland. These specimens were transported in fresh sea water to the 90 cm. X 90 cm. X 45 cm. fibreglass holding tanks and maintained in running sea water at ocean temperatures for one week. The sculpins were not fed during this interval. Two weeks before the experiments began, thawed pieces of capelin were fed ad libitum and 12 of the most active feeders were chosen as experimental fish. The mean wet weight of these fish was 457 grams (379 - 565 gm.) and the mean total length was 34.4 cm. (32.5 - 36.5 cm.). After the initial selection, the 12 experimental fish were transferred to the experimental tank and starved for 14 days before the first experiment began. The same fish were used for each of the five replicates, with 8 to 12 days starvation between each feeding experiment.

The 220 cm. X 220 cm. X 30 cm. experimental tank was divided into 12 chambers using wooden frame partitions covered with a fine nylon mesh, (see Figure 2). This separated each experimental fish but allowed a continuous flow of sea water throughout the tank. A black plastic canopy covered the entire tank to eliminate interference from laboratory lighting. Beneath this canopy, three different light conditions

Figure 2. Experimental tank for light/dark feeding study.

A. Side view of tank showing some of the partitioned regions.

B. Close view of black canopy and darkened slats covering some partitioned regions.


65
A
B

were established, dividing the tank into three regions each with four partitioned areas. At one end of the tank, a 12 hour light/dark cycle (designated C for cycle), was set up for one set of four partitioned areas. A 25 Watt incandescent bulb with a light green plastic shade was placed approximately 95 cm. above the water surface. Transitions from one light condition to the other occurred gradually. The opposite end of the tank was set up in the same manner except there was no cycle, but a continuous light environment (designated L for light). The middle four partitioned areas were completely blacked out to provide a continuous dark condition (designated D for dark). The wooden mesh partitions in this middle section were sheeted with black plastic, darkened wooden slats were laid across the top of these partitions, and black plastic sheets hanging from the canopy roof to the darkened slats prevented light entering from either of the lighted ends of the experimental tank. There was no attempt to record light intensities in the dark compartment, and therefore, every possible source of light may not have been successfully eliminated. Despite this weakness in the apparatus, light intensities were substantially decreased in these partitioned regions, and the experiment does provide important data on the effect of light on sculpin feeding success. Four experimental sculpins were acclimated under each of the three light conditions, C-cycle, L-light, and D-dark.

Preliminary observations indicated that thawed capelin pieces

(10 - 15 gm. each), were consumed immediately when dropped into the partitioned areas. The sinking motion of the food probably released the feeding response. To eliminate this variable, a black PVC two inch diameter hollow cylinder was placed in the partitioned area for each feeding session. One end of the cylinder extended above the water level and capelin pieces could be added and allowed to settle without visual perception by the sculpin. A 5 minute delay between cylinder placement and capelin addition allowed the sculpin to become accustomed to the presence of the feeding cylinder. After the capelin settled, the cylinder was quickly removed with no apparent disturbance to the experimental fish. Two of the four sculpins in each light environment were fed in this manner at 10:00 A.M. and the remaining two under each condition were fed at 10:00 P.M. that same night. The number of capelin pieces consumed after 1 minute, 10 minutes, and 2 hours from the initial feeding was recorded. A small penlight allowed inspection of partitioned areas under dark conditions with no illumination of adjacent areas. Feeding success was expressed as a percentage of the number of pieces given, i.e. Feeding Success = # pieces eaten / # pieces given. In this way, feeding success at different times of the day as well as under different light conditions could be compared.

A continuous Rustrak temperature recorder monitered the sea

water flow at the intake and the outlet ends of the experimental tank. The sea water was maintained at ambient ocean temperatures throughout all 5 replicates. Although temperatures rose from 2.8 °C. to 12.0 °C. during these experiments, water temperatures during each replicate only varied by 1.0 °C.

(ii) Oxygen Bomb Calorimetry

The predominance of capelin in longhorn stomachs during the capelin spawning period and the seasonal nature of this particular feeding raises the question of how this food resource compares with others in terms of energy. When the longhorn's diet changes from mainly fish to mainly invertebrate, what are the energetic changes that accompany the dietary change ? To investigate this, the caloric content of certain major sources of food energy and some potential prey of the longhorn sculpin were determined.

Capelin were hand netted from the sand/pebble beach at Middle Cove during their spawning period in July 1973, and were frozen within 2 hours of collection. During the fall of that year, 8 of these capelin were thawed, blotted, and weighed. They were then dried to a constant weight in an 80.0 °C. oven and powdered using a mortar and pestle. Approximately 1 gram samples, three per specimen, were pelletized and combusted in a Parr adiabatic oxygen bomb calorimeter following the method in the Parr manual (Parr Instrument Co., 1964).

Collections of the spider crab (Hyas araneus), sea urchins (Strongylocentrotus drobachiensis), and scale worms (Family Polynoidae) were made in Dyer's Gulch, Logy Bay in January 1974. These organisms were weighed live after blotting, then dried to a constant weight in an 80.0 °C. oven. Organisms of each group were ground collectively using a mortar and pestle, then powdered in a carbon steel ball and mill/paint shaker apparatus; a piece of equipment used by geologists to crush small rock samples. Sea urchin tests were removed before the weighing and powdering procedure. Whole crabs including the shell were used in these caloric determinations. Samples of approximately 1 gram were taken from the homogenous mixtures and pelletized, then combusted as outlined in the previous paragraph. Large amounts of ash remained after each combustion of the crabs due to the calcareous exoskeleton ($CaCO_3$). Assuming all ash to be $CaCO_3$ and applying the correction of 0.137 calories per milligram of $CaCO_3$ given by Paine (1966), allowed a correction for endothermy to be applied to this group. Appropriate corrections for the length of fuse wire burned, acid formation, and the energy equivalent of the calorimeter were made.

All determinations were within 1.2 % of the mean caloric value for each specimen. A variation up to 7.6 % occurred between the individual capelin, most probably due to the presence of large quantities

of roe in the female specimens. However, caloric values for each capelin were all within the 1.2 % margin.

RESULTS

I. QUALITATIVE BEHAVIOURAL DESCRIPTIONS

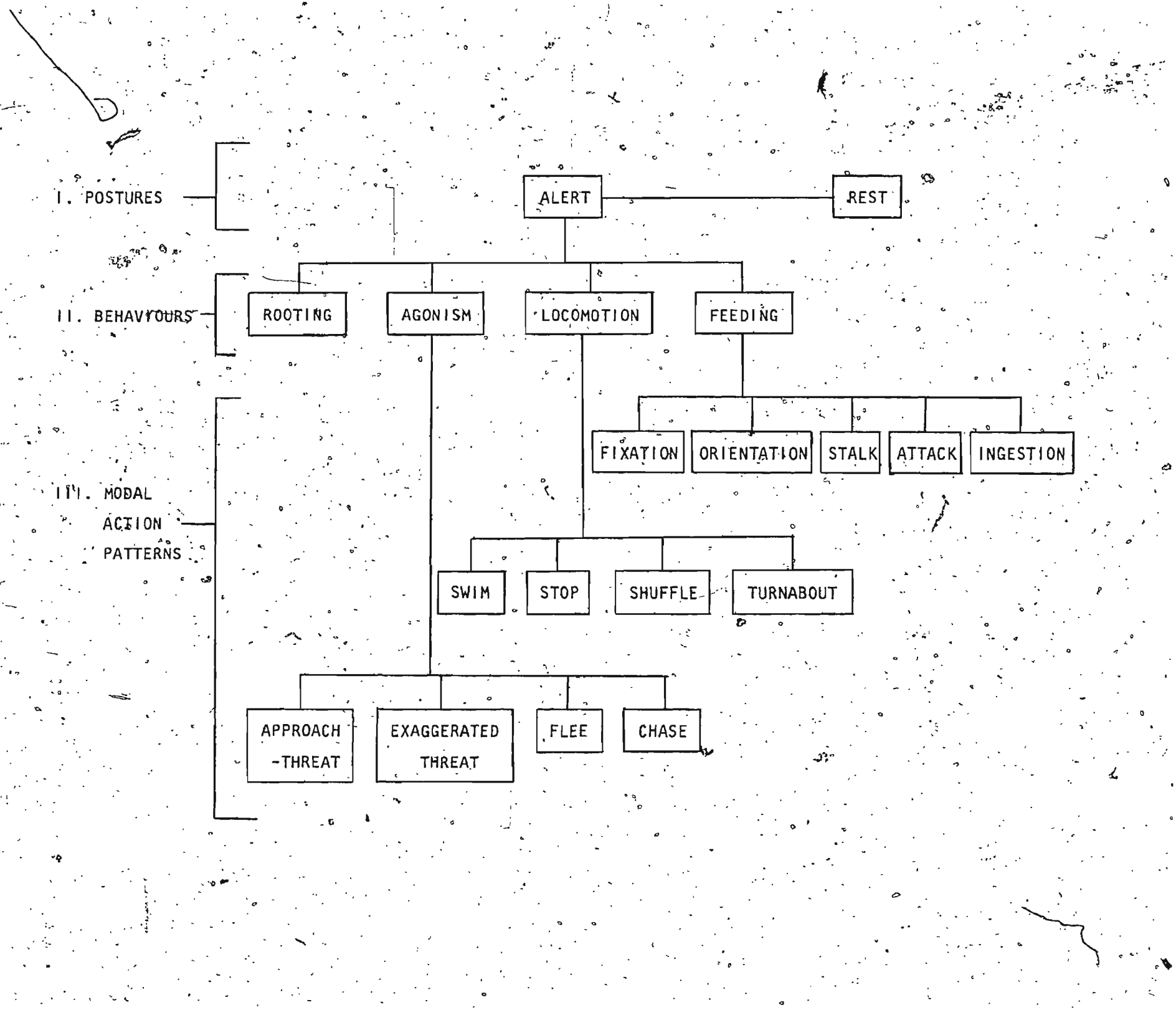
Almost 16 hours of direct daylight observations at St. Phillips and Outer Cove have provided a fairly comprehensive picture of the fundamental postures and associated behaviours which constitute a longhorn sculpin's daily activity. A graphic presentation of these activities is given in the behavioural profile, Table 1. Barlow's (1968) term Modal Action Pattern (M.A.P.) is used to describe the basic observable units of each behaviour. Reproductive behaviour is not described as longhorns spawn offshore in the winter and these were inshore summer observations.

Detailed descriptions of an organism's posture would be incomplete without incorporating information on the apparent function of the observed behaviour to which that posture appears related. Hence, the nomenclature used to describe the longhorn's postures are in fact directly related to the apparent behaviour observed accompanying that posture.

A. BASIC BODY POSTURES

There were two fundamental body postures observed which in their various forms are clearly distinguishable. The REST position is an invariant posture which is not commonly observed but nevertheless

Table 1. Behavioural profile of Myoxocephalus octodecemspinosus, showing the 2 fundamental postures and the 4 observed behaviours with their associated Modal Action Patterns.


I. POSTURES
ALERT
REST
II. BEHAVIOURS
ROOTING
AGONISM
LOCOMOTION
FEEDING
FIXATION
ORIENTATION
STALK
ATTACK
INGESTION
III. MODAL ACTION PATTERNS
SWIM
STOP
SHUFFLE
TURNABOUT
APPROACH -THREAT
EXAGGERATED THREAT
FLEE
CHASE

constitutes a basic body postion, (see Figure 3). In this posture, the sculpin is nestled in rock crevices or in the furrows of sand patches. The body is low and follows the contours of the substrate. The head is down, resting on the bottom and the fins are adducted to the body and folded. In this position the sculpin is motionless and unresponsive unless handled roughly or physically disturbed. The longhorn is still, and although the eyes are open, they do not move about. Generally, the sculpin exhibits no movement or activity except for tail sway in a heavy surge.

The second basic body posture is the ALERT position, (see Figure 4). In its most fundamental form, the body is at an angle to the substrate with the head, remaining longitudinal to the body axis, elevated above the substrate. Extension of the pectorals and possibly the pelvic fins serve to raise the head and anterior portion of the body. Most of the ventral surface of the body is in contact with the bottom and the fins are either partially or completely extended, depending upon the degree of activity. Since sculpins in this posture quickly respond to external stimuli, and numerous behavioural units have been observed associated with this posture, it seems that the ALERT position represents the sculpin in its active state. Sculpins actively responding to an external stimulus change their body postion. The entire body becomes elevated above the substrate with only the pelvic, pectoral, caudal, and anal fins in contact with the bottom.

Figure 3. REST posture showing sculpin nestled among the rocks.

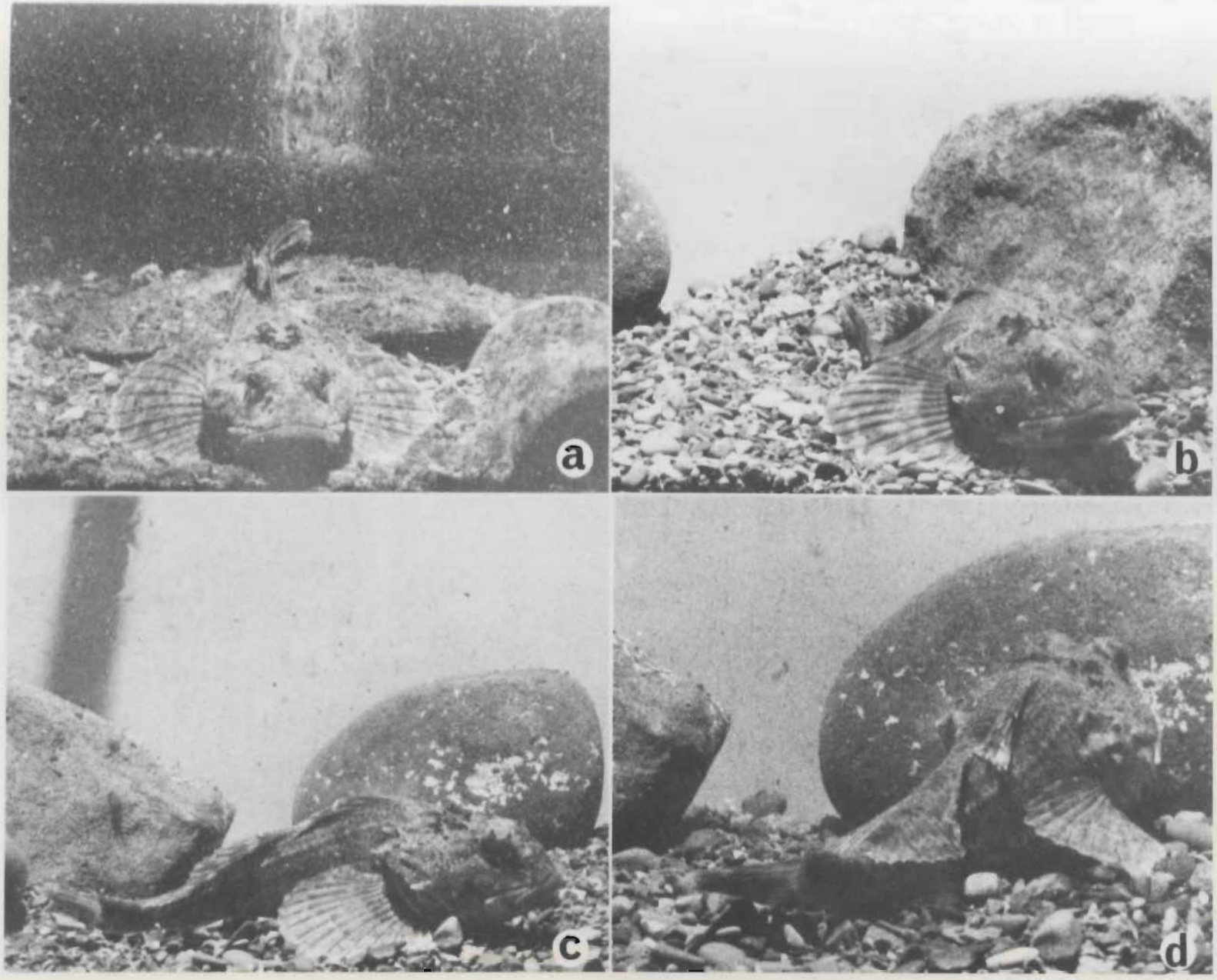
Figure 4. ALERT posture.

(a) front view showing elevated head and extended pectoral fins.

(b) front-side view showing elevated head and extended pectoral fins.

(c) side view showing elevated head, extended pectoral fins, and slightly extended dorsal spines.

(d) rear view showing elevated head with tail region in contact with substrate.


a
b
c
d

These fins spread out and extend to support the body, (see Figure 5).

B. BEHAVIOURS

There are four recognizeable behaviours in the daily activity of the longhorn sculpin. These were termed rooting, agonism, locomotion, and feeding. Each is associated with the ALERT posture.

(1) Rooting Behaviour

This peculiar behaviour was only elicited by sculpins on a sand substrate. The longhorn rotates longitudinally about 90° to one side exposing its pale ventral surface. The body then undulates against the sand in a rapid series of jerky movements. The rooting series ends with the sculpin in a normal ALERT posture. This behaviour is usually repeated two or three times during a single swim. It has also been observed to begin from an immobile position, although it usually occurred during swimming. The sand is distured into a large cloud after the rooting behaviour.

This behaviour occurs rarely, having been observed only 9 times while observing 3 different individuals at Outer Cove. This behaviour was not observed at St. Phillips.

(2) Agonistic Behaviour

Distinct agonistic interactions between individual longhorns were observed at St. Phillips. Although sculpins were found at high densities at Outer Cove, no agonism was noted at this location. The

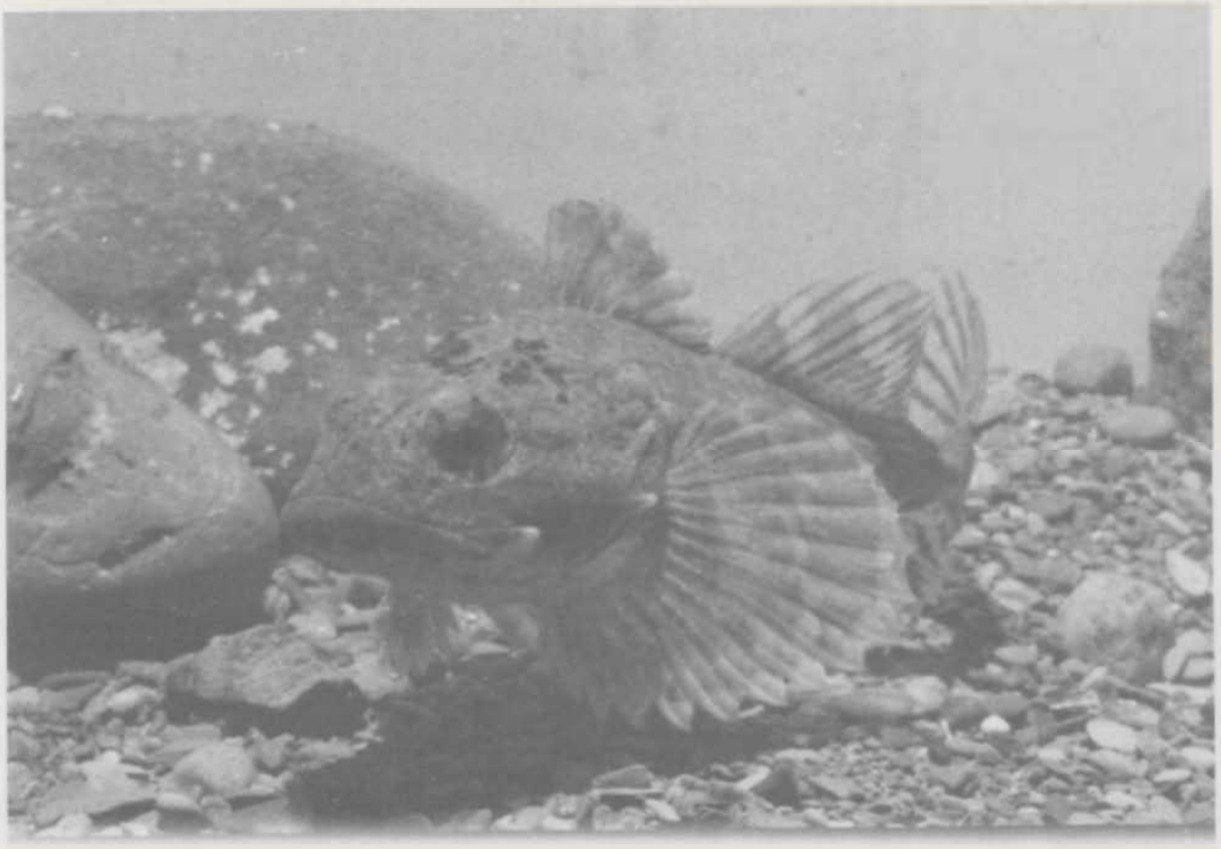
Figure 5. ALERT posture, sculpin actively responding to a stimulus.

Photograph A. shows body elevation with pectoral and pelvic fin support.

Photograph B. shows fin extension and body elevation.

A

B



frequency of occurrence of this behaviour was very low and with so few observations, a detailed analysis of its Modal Action Patterns was not possible. Despite this drawback, certain details were evident and provide a basis for further research into this behaviour.

Most of the 9 single interactions observed had a simple stereotyped pattern. The dominant and subordinant fish are both in the ALERT position. The aggressive longhorn with erect dorsal spines and extended fins, quickly swims towards the anterior of the second fish and approaches from the side or head on. The dominant fish approaches to within one metre of its subject before the subordinate sculpin quickly pivots away from its aggressor and flees. After a swimming chase with some turns and of a variable distance, the aggressor abandons pursuit and returns to the general vicinity where the agonism originated. It was not unusual for the subordinate fish to return, only to be chased away again by the same aggressor.

The basic units of the behaviour then, appear to be the approach, which incorporates a threat, the flee, and the chase. No submissive actions apart from fleeing, were observed.

On one occasion, a variation of this behaviour was observed. A longhorn previously observed to be aggressive, approached from behind to within one third of a metre from a second sculpin. When the approached fish did not flee, the aggressor continued to advance, swam alongside,

and settled in front of it. Immediately, the aggressor shook its body, quivered from side to side, and repeatedly opened and closed its pectoral fins. At this point, the second fish quickly pivoted and swam away with the typical flee response. This unusual action on the part of the aggressor could possible be an exaggerated threat display. No flee response ensued when the threatening approach was elicited, so a more direct interaction was necessary in the encounter.

There appears to be no relationship between size of the longhorn and the outcome of the encounter. Small sculpins were seen to be successful aggressors over larger ones and vice versa.

While using dead capelin to attract cunner to the entry hatch of LORA I at night, it was usual for 4 or 5 sculpins to be attracted also. Under these conditions, agonistic behaviour was observed. On one occasion, two longhorns dominated the lighted region beneath the hatch, while 3 or 4 others remained in the periphery. These peripheral fish occasionally ventured into the lighted region, only to be chased away by one of the two aggressors, following which the aggressor quickly returned to the lighted area. These two dominant sculpin did not display any agonictic behaviour towards each other, despite their close proximity.

Although sculpins are attracted to large feeding aggregates of cunner and agonism is common under these conditions, agonism is not

restricted to feeding circumstances. Aggressive interactions have been observed between individuals not involved in any apparent feeding behaviour and not attracted to large groups of other feeding fish. This, together with the fact that numerous longhorns in the same general area do not exhibit agonism, make it difficult to suggest the purpose of this behaviour. More extensive observations will be required to determine the functional significance of longhorn sculpin agonistic behaviour.

(3) Locomotor Behaviour

Locomotor behaviour is a common diurnal activity of M. octodecemspinosus. This behaviour is characterized by four Modal Action Patterns; swim, stop, shuffle, and turnabout.

(i) Swim

From an ALERT position, periods of continuous swimming or swims are initiated. A conspicuous extension of the caudal and dorsal fins immediately precedes the onset of a swim. This perceptible alteration of fin position also precedes the shuffle and turnabout M.A.P.'s of locomotor behaviour. It is possible that a raised level of excitation preceding any motor activity causes such a fin change, since fin extension seems characteristic of the active sculpin. Movement of the extended pectorals elevates the body completely from the substrate, and undulations of the tail and body

propel the fish forward. During the swim, fins are usually adducted to the body, although during a direction change, i.e. a turn, the pectoral fins extend. Swims are usually close to the substrate, excursions up into the water column occurring only during a feeding response. The pectoral fins extend at the termination of a swim and the sculpin settles to the bottom in an ALERT position. On rocky bottoms, swims are mostly short trips from one boulder to another. An immobile fish will suddenly initiate a swim from a large rock and alight a short distance away (usually a metre or so), on another rock. It is not uncommon for a longhorn to initiate a swim from a large boulder, extend all fins, then slowly glide or coast to the pebbled substrate below, again ending in an ALERT posture. Longer swims up to and exceeding seven metres have also been observed on rocky substrates but these are more common on a sandy bottom. These longer excursions are characterized by steady continuous swimming with numerous direction changes.

(ii) Stop

This M.A.P. occurrs between a series of swim M.A.P.'s. Sculpins are in the ALERT posture and are stationary. A conspicuous action during this M.A.P. is the flush. The mandibles extend, the gill opercula dilate, and the fish pumps in a spasmodic jerk. This action has been observed after ingestion and appears to flush bits of food

from the buccal cavity out through the gills. However, this action has also been observed to occur when no feeding was apparent. Tail sway is not an uncommon occurrence in a heavy surge and gill cover movements are also detected as movements associated with the stop M.A.P.

(iii) Shuffle

This M.A.P. also occurs between swims. The immobile fish suddenly extends its pectorals completely and uses them in conjunction with repeated body twists to resettle. The axial direction of the body changes only slightly if at all. The function of this M.A.P. is not apparent, but it appears to readjust the fish's position on the substrate.

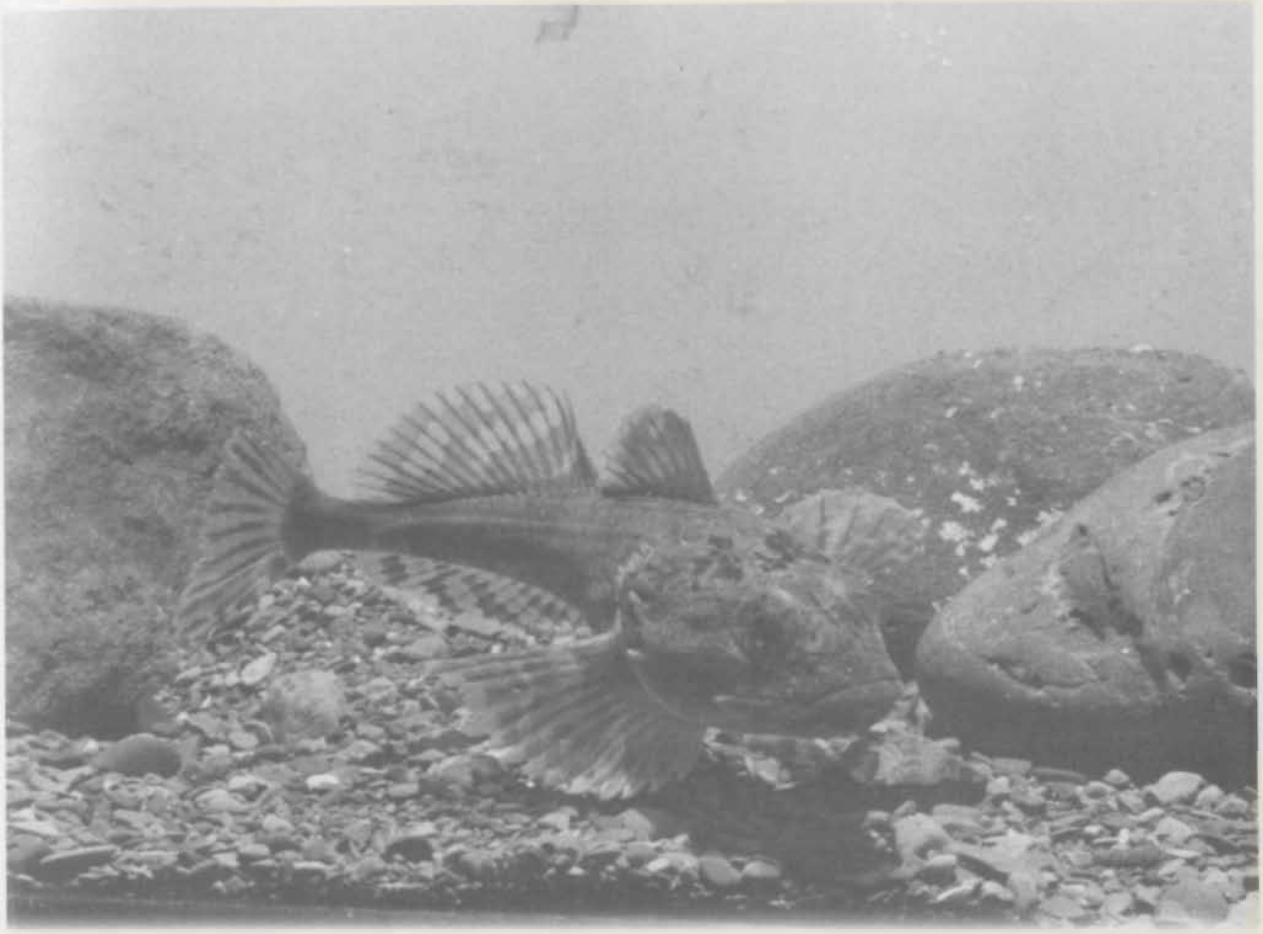
(iv) Turnabout

Complete changes in axial direction occur in the fourth M.A.P. of locomotor behaviour, the turnabout. Stationary fish extend their pectorals completely and rotate them with a twist of the body. This raises the body completely from the substrate and changes its direction, (see Figure 6). This form of repositioning may increase incoming stimulation by changing the scanning field of the sculpin.

(4) Feeding Behaviour

The feeding behaviour of M. octodecemspinosus is a stereotyped behaviour characterized by a sequence of five distinct Modal Action

Figure 6. Turnabout Modal Action Pattern of locomotor behaviour showing body twist and elevation with all fins extended.



Patterns. Clearly recognizeable behavioural units; fixation, orientation, stalk, attack, and ingestion constitute the complete sequence of the feeding behaviour.

(i) Fixation

The sculpin in an ALERT posture quickly rotates its eyes towards and 'fixes' upon the moving object. If this potential food is above the sculpin in the water column, the head tilts to one side, cocked towards the food. Immediately preceding the next M.A.P., the dorsal spines erect and serve to extend this fin. The extended fin position is indicative of a reponsive fish about to change its pattern of activity, in this case, to orient towards the food.

Visual fixation of the food appears to be the food detection phase of the feeding behaviour. However, feeding behaviour not initially dependent upon vision has been observed in the laboratory. Sculpins elicited feeding attacks on the black feeding cylinder during the light/dark laboratory experiments. The initial response was to the placement of the tube and probably involved visual cues. However, feeding responses were again initiated when capelin pieces were dropped into the cylinder. As these reponses were delayed, sculpins were not reacting to the presence of the experimenter, but to the capelin. Possibly olfactory or pressure stimuli were detected. Whatever the sensory stimulus involved, visual fixation was not observed, only a

swift orientation to the cylinder by axial repositioning. This seems to indicate that a visual fixation is not necessary for the feeding sequence to be completed. Some form of sensory fixation must have occurred though, as a directional orientation occurred.

(ii) Orientation

This M.A.P. aligns the sculpin so that it faces the food object. It is accomplished by a partial turn or a complete turnabout towards the food. These actions occur in the same manner as was described for the turnabout M.A.P. of the locomotor behaviour. It is possible that these actions are not M.A.P.'s of locomotor behaviour but are in fact components of an incomplete feeding response. The alternative already discussed is that such actions serve to change the longhorn sculpin's scanning field. More observations of locomotor and feeding behaviour are needed to clarify this point.

In any event, orientation is a discrete M.A.P. of the feeding behaviour, and is distinct from the relatively immobile fixation M.A.P. If a longhorn fixates upon a prey and is already in the correct axial position, no orientation occurs; stalk actions immediately follow the fixation.

(iii) Stalk

Stalking sculpins in the ALERT posture have been observed positioned from approximately 10 cm. to 0.5 m. from the prey. The predator is very responsive and all fins are extended. If the stalk M.A.P.

is of a long duration, various degrees of fin extension are apparent, but the body and head are always elevated and dorsal spines erect preceding any change in position.

During a stalk, this behaviour is interrupted by sudden short advances towards the prey. These lunges cover several centimetres and apparently position the predator closer to its prey, possibly to increase its success at the final attack. It is also possible that these lunges are "intention movements" indicating the direction in which the behaviour of the fish will proceed. A second "intention movement" type of motor activity is the start; a sudden forward lurch. No distance is covered during these starts and they clearly indicate the active nature of the predator.

The stalk M.A.P. is usually a prolonged pattern having been observed for periods exceeding 30 minutes without an attack. However, the fixation, orientation, and stalk M.A.P.'s can occur in rapid succession during feeding responses to swiftly swimming prey for instance. Generally, it appears that during the stalk, the predator waits for the prey to expose itself or for some other stimulus to initiate the next M.A.P. of the feeding behaviour.

(iv) Attack

The attack M.A.P. differs according to whether the prey is on the substrate or in the water column. On the substrate, the predator suddenly lunges towards the prey. This action covers a short distance,

usually less than half a metre, and is characterized by its rapidity and its termination by ingestion attempts.

When the prey is in the water column, a locomotory attack occurs. It begins with an extension of the pectoral fins and erection of the dorsal spines, and a slow swimming ascent towards the prey. As the food is approached, the sculpin swiftly accelerates to the final quick lunge of ingestion. After an attack is initiated in the water column, it is common for the sculpin to lunge a number of times at its prey if the first lunge is unsuccessful. Such multiple feeding lunges have been observed when longhorns attacked aggregates of cunner at St. Phillips. In the midst of the cunners, frenzied turns and twists with ineffectual lunges lead to an unsuccessful attack. These observations suggest that the sculpin under such conditions is disoriented and unable to direct its feeding attack at a specific prey.

(v) Ingestion

Ingestion is the last M.A.P. of the feeding response. A few centimetres from the prey, the mouth opens and food is sucked into the buccal cavity. Swallowing was not detected after the food was swept into the mouth. Incidental debris, sand and/or pebbles are expelled through the mouth after ingestion. When larger prey are ingested, (eg. capelin), a form of swallowing does occur. Gulping, consisting of a slow extension and retraction of the jaws gradually forces the prey down the esophagus. The large pharyngeal tooth pads

are probably important in this form of ingestion. If ingestion is not successful in a mid-water attack, the sculpin slowly settles to the substrate into an ALERT posture. The predator is still very responsive and may even initiate a second attack. On some occasions, the unsuccessful sculpin settles and turns away from the feeding site. No further responses are elicited. If the food is too large to be ingested, the sculpin "bulldogs" the food with a side to side movement of the body. The food is part way in the mouth, and rapid jerks from side to side occur, as if to free or break up the food.

The feeding behaviour can be interrupted before completion of the ingestion M.A.P. Sculpins attacking prey in the water column have abandoned the attack to avoid an interfering light beam shone by a diver. Also, sculpins have been observed stalking large crabs (Cancer sp.) for long periods, then abruptly initiating a swim and leaving the site of the crab.

C. GENERAL FEEDING OBSERVATIONS

A form of social facilitation among the sculpins appeared during feeding: When Ulvaria or Pholis are released, one sculpin may initiate a feeding attack, but is soon accompanied by several more. When there is much activity in the form of repeated ingestion attempts or multiple feeding lunges, for example when food is released among a group of sculpins, numerous other longhorns converge on the feeding site. One sure way to double or triple the number of sculpins

in an area is to establish a situation which stimulates feeding. This same phenomenon has also been observed during feeding in the laboratory. A dozen immobile sculpins on the tank bottom do not all respond immediately to the introduction of a few pieces of capelin. One or two immediately attack and ingest the capelin, and this stimulates the others resulting in a frenzy of activity, with sculpins attempting to ingest one anothers' fins. These repeated attacks on each other suggest that the longhorns do not visually discriminate food from non-food, but respond primarily to movement. These fish respond to and actually ingest pieces of paper and bits of algae swaying in the current. These items are quickly ejected, and it is not uncommon to see the same fish ingest the same item again. Sculpins have also been observed feeding selectively on dead capelin which moved slightly with the water flow. Observations such as these support the statement that the longhorn is a scavenger as well as a bottom predator.

The longhorn sculpin does not seem to be a very successful predator of the rock gunnel. When this prey was released at the surface at Outer Cove and began to swim to the bottom, numerous longhorns responded to and attempted to ingest it, but were unsuccessful. The prey undulated among the lunging sculpins and successfully reached the substrate cover. Pholis swimming across bare sand patches were chased by sculpins, but easily reached the rocks fringing the sand before the sculpins could catch them. Some of the predators near the site of

concealment exhibited the stalk M.A.P., but no ingestion of this prey occurred. Releasing this prey from the surface may not be a feeding situation normally encountered by the sculpin, but it indicates the inefficiency of the longhorn as a predator of this small benthic prey. Also, on several dives, longhorns were observed within one half a metre of exposed Pholis and no feeding occurred. The movement of individual flounder swimming on the bottom near sculpins did not elicit any feeding behaviour either. What releases a feeding attack if it is not just movement remains to be determined.

II. QUANTITATIVE ANALYSES OF LONGHORN SCULPIN BEHAVIOUR

The frequency of occurrence of 3 specific behaviours, (feeding, rooting, and agonism), and 1 M.A.P. (stalk), was determined from the individual observation data of both locations. A Multivariate Analysis of Variance computer program (MANOVA, Clyde 1969), was used to assess the effects of location (Outer Cove and St. Phillips) and time (A.M. and P.M.) on the occurrence of these behaviours and this M.A.P. Significant differences between the occurrence of the 3 behaviours or the 1 M.A.P. in the morning and in the afternoon would be evidence of a diel pattern in the sculpin's activity. However, time had no significant effect on the frequency of occurrence of these measures, ($F = 0.840$, $P < 0.519$). This is attributed to the absence of the agonistic behaviour at Outer Cove, and the absence of the rooting

behaviour at St. Phillips. However, conclusions about the diel nature of sculpin activity based on this analysis alone should not be considered definitive. The frequency of occurrence of the four measures was so low, that applications of the MANOVA test are subject to criticism. Without more complete data, conclusions on the effects of location or time on behaviour should not be made.

Quantification of locomotor behaviour was achieved by expressing the observed number of excursions and number of turns as a function of the observation interval. As a result, for the experimental and non-experimental observations, the # of excursions/minute and the # of turns/minute are two quantitative measures that can be statistically analyzed. To assess the effects of location and time on these two measures of locomotor behaviour and to compare the experimental and non-experimental behaviours, the MANOVA program was again used. Non-experimental and experimental data from St. Phillips and Outer Cove are presented in Appendix 1 and 2 respectively.

There appears to be much variability in these two measures of the locomotor behaviour of non-experimental fish. This is apparent when the standard deviations and mean activity values in Table 2 are compared. Neither location ($F = 2.938$, $P < 0.077$), nor time ($F = 0.538$, $P < 0.592$), had a significant effect on the locomotor activity as represented by excursions and turns. This is evidence suggesting that no

Table 2. Quantified locomotor behaviour of non-experimental longhorn sculpins at Outer Cove and St. Phillips.

	OUTER COVE		ST. PHILLIPS	
	A.M.	P.M.	A.M.	P.M.
Mean number of excursions/minute	0.109	0.151	0.350	0.245
Standard Deviation	0.070	0.223	0.606	0.279
Mean number of turns/minute	0.103	0.055	0.360	0.273
Standard Deviation	0.076	0.059	0.598	0.289
Total number of fish observed	7	8	3	6
Observation time, total minutes	365	265	100	220

MANOVA.....F values Location effect .... $F = 2.938$ $P < 0.077$

Time effect ..... $F = 0.538$ $P < 0.592$

Location/Time ..... $F = 0.408$ $P < 0.670$

diel activity pattern exists in the longhorn sculpin's behaviour, since the number of excursions and the number of turns per minute are randomly distributed over the morning and afternoon daylight hours. However, the power of the F test needs to be increased with the addition of more individual observations for each time and location. With such a high degree of variation about the mean activity values and the small sample size, this data may not be representative of the population.

Only two control fish were observed for the St. Phillips experiment due to difficulties in making the caged sculpins ingest food. Despite this drawback, the experimental behaviour can be compared with the non-experimental locomotor behaviour of the longhorn. Table 3 compares the collapsed data (A.M. and P.M. data pooled), from the non-experimental observations of each site with the experimental observations. There was also much variation in the activity of the experimentally starved sculpins. Even with such variation, the locomotor behaviour of the experimental fish was more intense than for the non-experimental fish at both locations. Both the # of excursions/minute ($F = 5.984$, $P < 0.007$), and the # of turns/minute ($F = 13.265$, $P < 0.001$), were significantly higher than the values for the non-experimental fish. Thus, the experimental sculpins exhibited more locomotor activity than the non-experimental longhorns.

Table 3. Quantified locomotor behaviour of non-experimental and experimental longhorn sculpins at Outer Cove and at St. Phillips, (A.M. and P.M. data pooled for non-experimental data).

	NON-EXPERIMENTAL OUTER COVE	NON-EXPERIMENTAL ST. PHILLIPS	EXPERIMENTAL ST. PHILLIPS
Mean number of excursions/minute	0.131	0.280	0.619
Standard Deviation	0.165	0.378	0.433
Mean number of turns/minute	0.077	0.302	0.756
Standard Deviation	0.070	0.379	0.429
Total number of fish observed	15	9	7
Observation time, total minutes	630	320	278

MANOVA (univariate test).....F values Excursions/min. $F = 5.984$, $P < 0.007$

Turns/min. $F = 13.265$, $P < 0.001$

It is also apparent from Table 3 that longhorn locomotor behaviour is more intense at St. Phillips than at Outer Cove. The incorporation of the swimming activity of the agonistic interactions into the St. Phillips observations may account for this difference. No agonism was recorded at Outer Cove.

Traces of sculpin movements at St. Phillips, both non-experimental and experimental, are presented in Appendix 3. These maps clearly show an offshore movement by the experimentally starved sculpins. The non-experimental fish remained in the same general vicinity and showed no offshore tendency. Possibly, the caged fish, upon release, were escaping or avoiding the caged area. None of the tagged caged fish were ever recovered.

III. FEEDING PERIODICITY

(i) General Information

The stomach and intestinal contents of 37 longhorn sculpins were sampled over a single 24 hour period on July 2/3, 1973. Total lengths of the sculpins had a range of 26.5 - 43.0 cm., and live wet weights ranged from 237 - 888 gm. The sex ratio of the sample was 1:1, with 19 males and 18 females.

Observations during the collection dives indicated that the sculpins were not actively feeding upon living capelin. Instead, the longhorns were abundant on the long rifts of decomposing capelin that formed after the capelin had spawned and died. Numerous feeding

responses with the complete feeding behaviour sequence of M.A.P.'s were observed at these locations. Sculpins in the ALERT posture were common on the rifts and appeared to respond to the swaying motion of the capelin bodies in the water currents. During the interval between the 2400 hour and 0400 hour dives, aggregates of sculpins shifted from the capelin rifts to large sand patches a short distance offshore.

Capelin are in abundant supply during their spawning period and are a primary food source for the longhorn sculpin during this time. Thirty-four of thirty-seven stomachs contained food, and each of these contained at least one whole capelin with digested remains of others. Although capelin was the major dietary component, spider crabs, amphipods, fish eggs, and algal filaments were also found. These items, however, represented a negligible portion by weight of the stomach contents and were not included in the calculations.

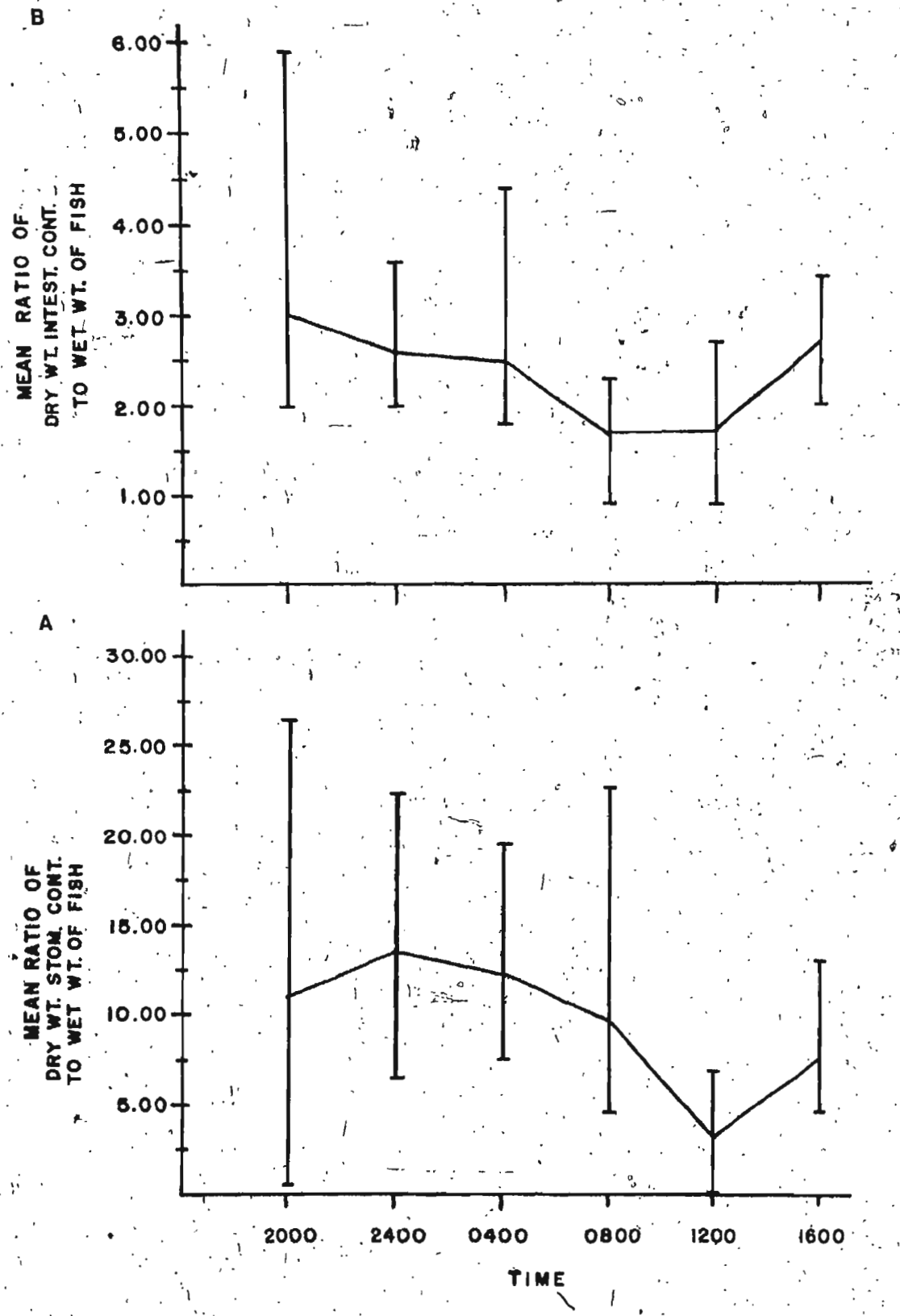
(ii) Measures of Cyclic Feeding

Three measures were used to determine changes in feeding intensity over the 24 hour period. Stomach contents, intestinal contents, and frequency of occurrence of digestive stages were statistically analyzed separately, and then compared for evidence of feeding periodicity.

The mean ratios of dry weight stomach contents (grams) per wet weight of fish (kilograms) for each sample time are presented in Figure 7A. A definite pattern is evident; maximum values of 13.5 gm/kgm at 2400 hours decreasing to a minimum of 3.3 gm/kgm at 1200

Figure 7. A. Mean ratio of dry weight stomach contents to wet weight of fish. Each value is the mean of six fish sampled at each time. Ranges for the means designated by the vertical lines.

B. Mean ratio of dry weight intestinal contents to wet weight of fish. Each value is a mean of six fish sampled at each time. Ranges for the means designated by the vertical lines.


B
6.00
5.00
4.00
3.00
2.00
1.00
MEAN RATIO OF
DRY WT. INTEST. CONT.
TO WET WT. OF FISH
A
30.00
25.00
20.00
15.00
10.00
5.00
MEAN RATIO OF
DRY WT. STOM. CONT.
TO WET WT. OF FISH
2000
2400
0400
0800
1200
1600
TIME

hours. This suggests a cyclic feeding pattern with the sculpin having intensified its feeding after 1200 hours. Sculpins appear to feed heavily all night and the level of feeding then falls off at sunrise. To test this hypothesis, an Analysis of Covariance using Clyde's (1969) MANOVA computer program, was used to analyze the data. Fish weight may influence the calculated ratios, so the wet weight of the sculpin was chosen as the covariate, while the stomach contents were the criterion. Mean dry weight values of stomach contents were compared for each of the six sample times. By determining the F ratio, the variance accounted for by the time of sampling was calculated according to the formula $\omega^2 = SS_{bg} - df(MS_{wg})/SS_t = MS_{wg}$, (Hays 1963). Time does not have a significant relationship to stomach content weight, ($F = 1.841$, $P < 0.136$), and hence the Null Hypothesis (H_o = time has no effect on sculpin feeding), cannot be rejected. Only 10.59 % of the variability of the stomach content weights is accounted for by the time variable. The large range about each mean value was caused by more than just time.

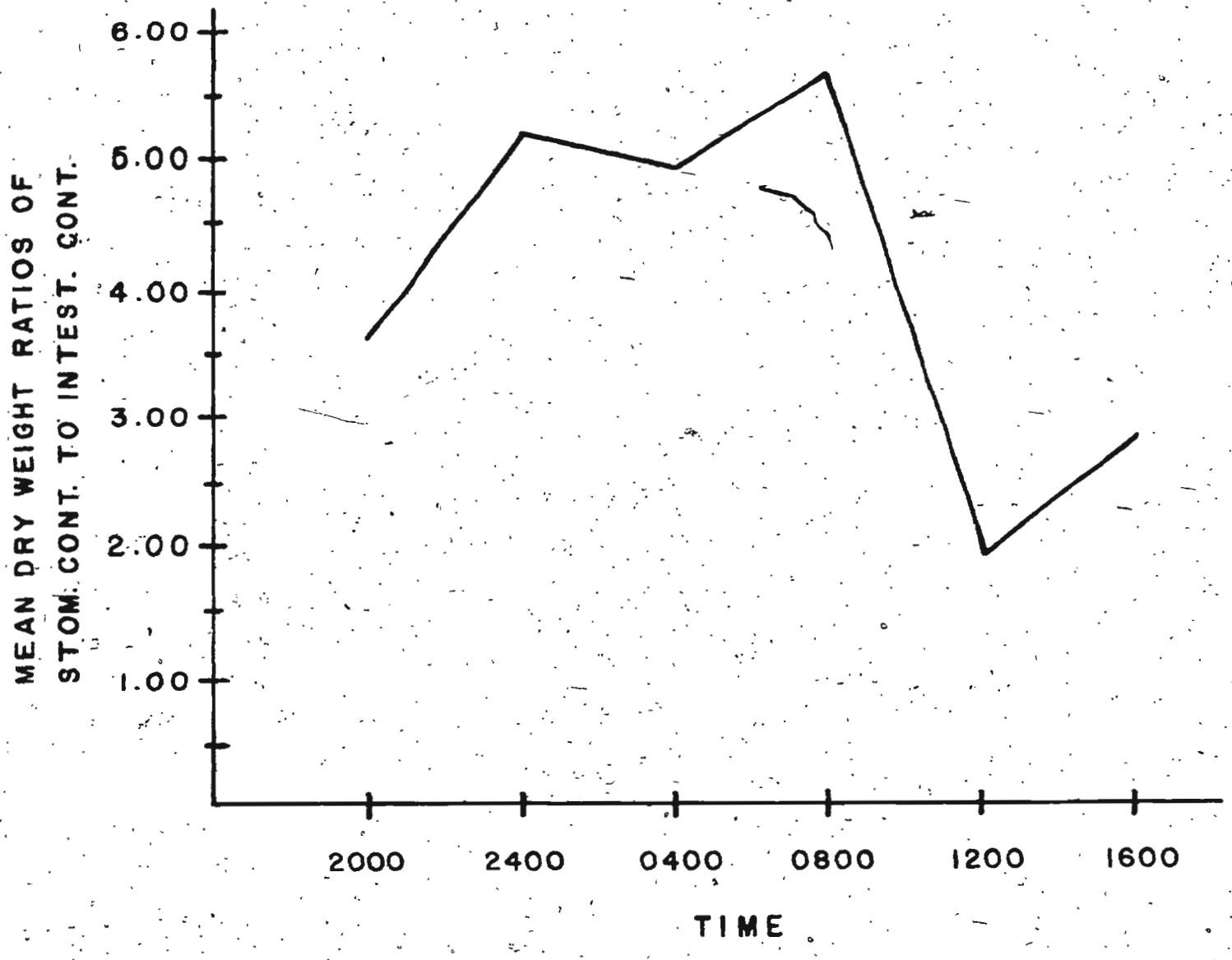
From Figure 7A, it can be seen that the mean weight of the stomach contents per kilogram of sculpin is considerably lower than that for the individual with the fullest stomach. The average stomach in the population was not completely filled, a phenomenon also noted by Mathur (1973) and Keast and Welsh (1968) in their studies of freshwater fishes. There may be a number of reasons for this. An

individual 'overeats' during one feeding period, then may consume correspondingly less at the next one. Alternately, metabolic needs may be adequately met by less than the maximum intake of food, feeding may be rhythmic, or the amount of food available in a given time may be limited, (Keast and Welsh 1968). As this sampling occurred during the capelin spawning period, a time of an over abundant food supply, and since time appears not to have a significant effect upon feeding, only the first two alternatives seem to be viable for the longhorn sculpin population.

The second measure of feeding periodicity, intestinal contents, display a similar trend in times of consumption as did the stomach contents. In Figure 7B, it is apparent that maximum values of 3.0 gm/kgm at 2000 hours decrease to a minimum of 1.7 gm/kgm at 0800 hours. There is a reduced amount of variability in this data and the same Analysis of Covariance employed to analyze the stomach contents indicates that time does have a significant relationship to intestinal contents, ($F = 2.646$, $P < 0.043$). However, the calculated F ratio is only just significant at the 0.05 level and time only accounts for 18.99 % of the variance in these samples. Feeding periodicity inferred from the intestinal content data would be suspect without a consideration of the factors which contribute to the bulk of the variance.

Figure 8 presents the ratio of mean dry weight stomach contents to the mean dry weight intestinal contents over the sampling period.

Figure 8. Mean dry weight ratios of stomach contents to intestinal contents. Ratios determined from values in Figure 7 A and B.


MEAN DRY WEIGHT RATIOS OF
STOM. CONT. TO INTEST. CONT.
6.00
5.00
4.00
3.00
2.00
1.00
2000
2400
0400
0800
1200
1600
TIME

This ratio increases over the interval from 1200 hours to 0800 hours, the same period that both stomach and intestinal contents decrease to their minimum values, (see Figure 7 A & B). This suggests that food was still entering the stomach up to 0800 hours, feeding stopped or was very infrequent at noon, and by 1600 hours had begun again, increasing thereafter. However, the changing stomach/intestinal content ratio is not just a function of the addition of food to the stomach, but also changes with evacuation rates. The value of this statistic as a measure of feeding periodicity therefore, is questionable without information about digestion.

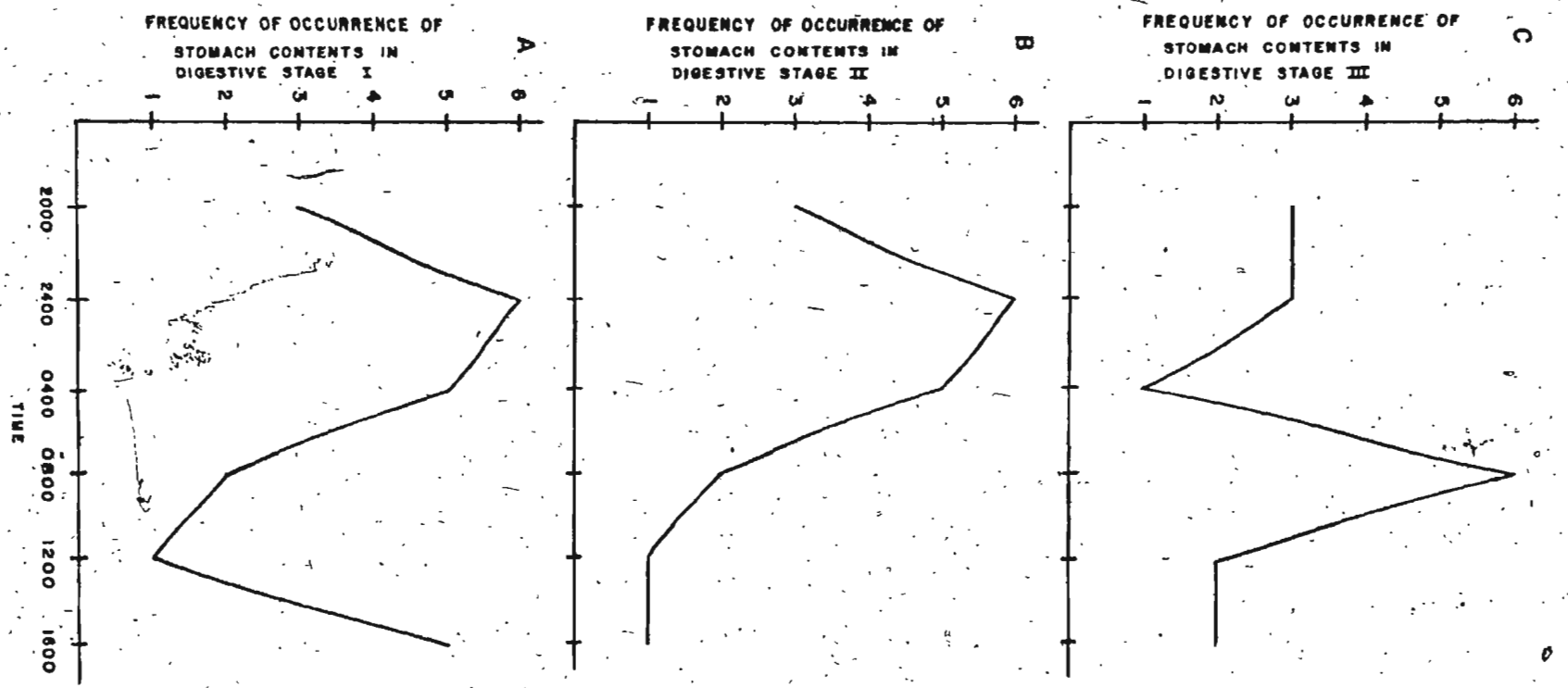
The third measure of feeding periodicity, frequency of occurrence of various stages of capelin decomposition, bear out quite well the feeding trends indicated by the stomach and intestinal content data. From Figure 9 A & B, it is apparent that the initial and mid-stages of digestion (stages I and II), are common at 2400 hours but become less frequent as the day progresses. These periods of high frequency of stages I and II correspond to periods when stomach and intestinal contents are peaking (see Figure 7 A & B). The final stage of digestion, stage III, has a different pattern altogether, (see Figure 9C). This stage is most abundant at 0800 hours, the time when early stages are not in common occurrence. It appears that this third measure of feeding periodicity also lends credence to the hypothesis of cyclic feeding by the longhorn sculpin. Early

Figure 9. Frequency of occurrence of the three digestive stages of stomach contents sampled during the 24 hour dive series. Each value represents the number of sculpins with capelin in that particular digestive stage at that sampling time.

A. Digestive stage I.

B. Digestive stage II.

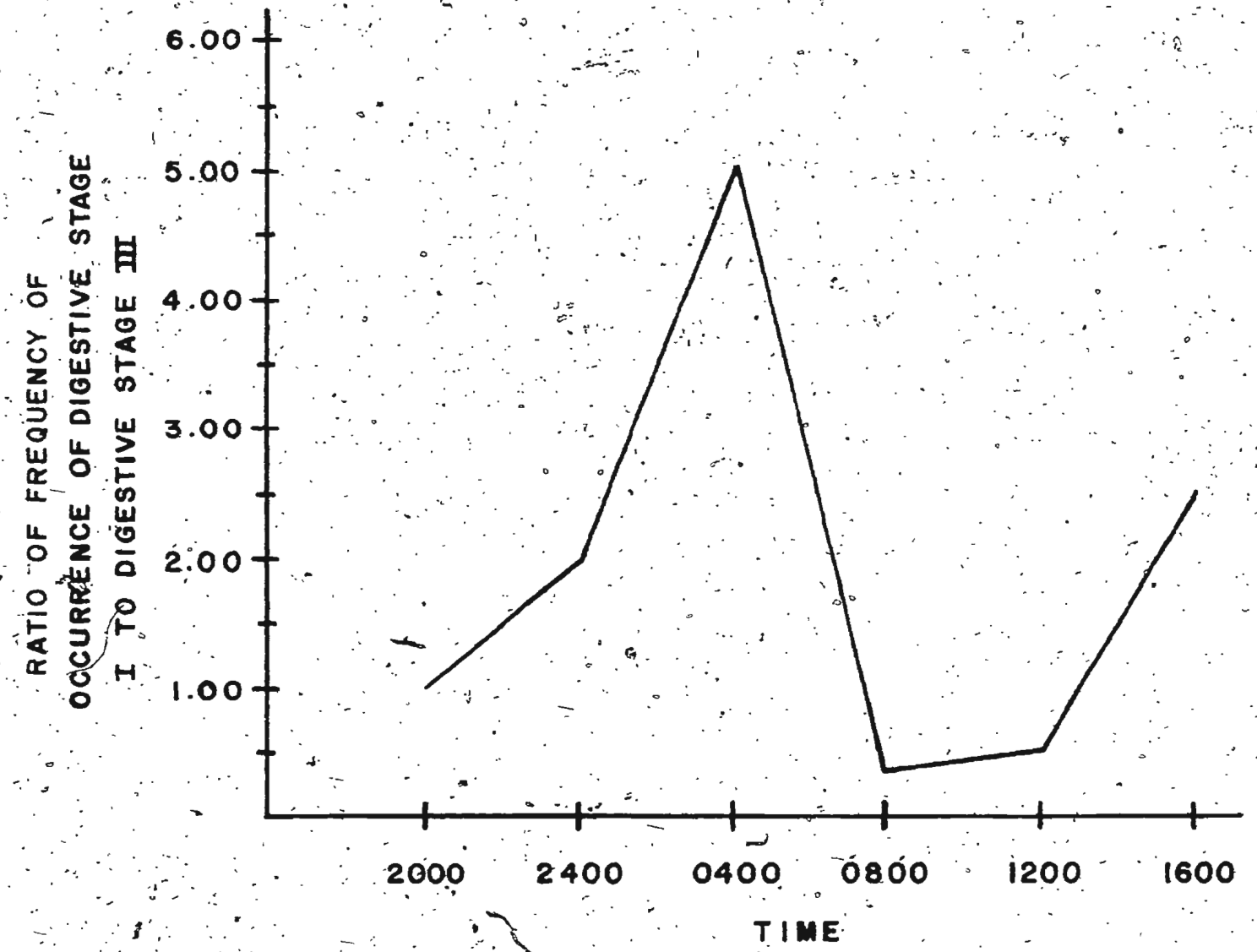
C. Digestive stage III.


FREQUENCY OF OCCURRENCE OF
STOMACH CONTENTS IN
DIGESTIVE STAGE I
A
FREQUENCY OF OCCURRENCE OF
STOMACH CONTENTS IN
DIGESTIVE STAGE II
B
FREQUENCY OF OCCURRENCE OF
STOMACH CONTENTS IN
DIGESTIVE STAGE III
C
1 2 3 4 5 6
TIME
2000
2400
0400
0800
1200
1600

stages of digestion become most common during the 1200 to 2400 hour period, with digestion to stage III occurring from 0400 to 0800 hours. Figure 10 represents changes in the ratio of the frequency of occurrenc of stage I stomach contents to stage III stomach contents over the 24 hour period. From 1600 to 0400 hours, there is a drastic shift in the condition of the stomach contents. This abrupt rise in the ratio suggests that feeding is greater than digestion during this period. Again, the same cyclic feeding pattern could be inferred from this data. However, a X^2 analysis of the frequency of occurrence of the three digestive stages over time (3 X 6 contingency table), produced no significant results, ($X^2 = 10.666$, $P < 0.3852$). Thus, despite the trends of feeding periodicity exhibited by the three digestive stages, time does not have a significant relation to the condition of the stomach contents.

Although time does not have a significant effect upon the three measures of feeding activity, there does exist a clearcut development of a maximum and minimum stomach content weight, and this criteria provides a basis for the calculation of the daily ration according to the method used by Keast and Welsh (1968) and Mathur (1973). The daily ration defined by Ricker (1946), is the quantity of food consumed each day by a fish, expressed as a fraction of percentage of its total weight. This method involves determination of the difference between the maximum and succeeding minimum mean weight stomach contents per

Figure 10. Ratio of frequency of occurrence of digestive stage I to digestive stage III for each sampling time. Ratios determined from values in Figure 9 A & C.


RATIO OF FREQUENCY OF OCCURRENCE OF DIGESTIVE STAGE I TO DIGESTIVE STAGE III
6.00
5.00
4.00
3.00
2.00
1.00
2000
2400
0400
0800
1200
1600
TIME

weight of fish. For the data on the longhorn sculpin shown in Figure 7A, the daily ration is determined to be 10.2 gm/kgm or 10.2 % of the body weight of the sculpin. This value may be considered minimal because some digestion must occur during feeding and there may be feeding when volumes of stomach contents lessen. This calculated daily ration for the longhorn sculpin agrees quite well with data from other sources, (see Table 4), although the sculpin's daily ration is at the lower range of these values.

Stomach content data for the longhorn and other marine fishes collected by Tyler (1971b) cannot be used to calculate a daily ration because his values are seasonal, not daily. However, his data is compared with the Outer Cove stomach data and with values for other marine fishes collected by Gibson (1973), (see Table 5). It is immediately apparent that large ranges occur in stomach content data for most marine fish, Pleuronectes platessa (plaice) being the only exception. Comparing values for the longhorn, it is evident that the maximum value from the 24 hour dive at Outer Cove, 13.5 gm/kgm, is much lower than Tyler's summer value of 40 gm/kgm. In fact, the Outer Cove maximum value only equates with Tyler's minimal winter value. Stomach contents of the longhorn during the winter were primarily mysid (Mysis stenolepis) and shrimp (Pandalus montagui), with values up to 14 gm/kgm; whereas during the summer, Meganyctiphanes norwegica (krill) was the primary prey with a peak in early summer caused by Clupea harengus (herring).

Table 4. Comparison of longhorn sculpin daily ration calculated from 24 hour dive data, with daily ration of other fishes.

SPECIES	HABITAT	TEMP. °C.	DAILY RATION % body wt.	SOURCE
Salvelinus fontinalus (brook trout)	fresh-water, lab.	16	2.0 - 6.0	Third Ed. New York State Hatch. Feeding Chart, 1952.
Lepomis macrochirus (bluegill)	fresh-water, lab.	25	3.0	Gerking, 1954.
L. macrochirus	fresh-water, natural	17.7-23.3	1.82	Seaburg & Moyle, 1964.
L. gibbosus (pumpkinseed)			1.03	
Pomoxis nigromaculatus (black crappie)			1.54	
L. macrochirus	fresh-water, natural	18 - 22	2.5	Keast & Welsh, 1968.
L. gibbosus			2.6	
Perca flavescens (perch)			2.0	
Fundulus diaphanus (killifish)			1.4	
Ambloplites rupestris (rock bass)			4.0	
Percina nigrofasciata (banded darter)	fresh-	15.0-22.8	2.6 - 4.9	Mathur, 1973.
Myoxocephalus octodecemspinosus (longhorn sculpin)	marine,	9.5	1.02	Jenkins, present paper.

Table 5. Comparison of longhorn sculpin stomach content weights with values for other marine fishes.

SPECIES	STOMACH CONTENTS MINIMUM	STOMACH CONTENTS MAXIMUM	SOURCE
	grams / kilogram		
Hippoglossoides platessoides (plaice)	3	45	
Gadus morhua (cod)	7	27	
Macrozoarces americanus (ocean pout)	5	25	
Melanogrammus aeglefinus (haddock)	2	12	Tyler, 1971b. - seasonal samples of stomach contents.
Pseudopleuronectes americanus (flounder)	2	14	
Raja erinacea (little skate)	2	15	
Urophycis teruis (white hake)	15	40	
Myoxocephalus octodecemspinosus (longhorn)	14	40	
Pleuronectes platessa (plaice)	0.75	2.0	Gibson, 1973. - daily summer samples.
M. octodecemspinosus	3.3	13.5	Jenkins, present study. - daily summer samples.

Stomach content values of up to 40 gm/kgm were found during the krill and herring summer peak, (Tyler 1971b). It is evident from these figures that offshore populations of M. octodecemspinosus ingest different kinds of prey and contain substantially more food in their stomachs than the inshore populations of the longhorn sculpin in Newfoundland.

IV. CALORIC CONTENTS OF SELECTED MARINE ORGANISMS

Caloric values determined on the basis of dry weight samples are presented in Table 6. Calories per gram wet weight were calculated from dry weight values using the wet/dry weight ratios as a conversion factor. The mean caloric content per individual was calculated by multiplying the mean individual weight (grams) and the mean calories per gram dry weight (cal/gm dry wt.) for each species. Capelin (M. villosus) and scale worms (Polynoidae) had the highest caloric values, 5341 and 4396 calories per gram dry weight respectively, whereas the spider crab (Hyas araneus) had the lowest energy content, 2691 calories per gram dry weight.

Table 7 compares these values with those determined by other researchers. The caloric value for S. drobachiensis (sea urchin), 3458 calories per gram dry weight, is consistent with Reddin's (M.Sc. 1973) value of 3448 cal/gm dry wt., a difference of only 0.5 %. Brawn et.al. (1968), included the sea urchin tests in their determinations,

Table 6. Caloric content of invertebrate and vertebrate prey collected from Middle Cove and Logy Bay, Nfld., in July 1973 and January 1974. (Numbers in parentheses below sample size are number of combustions performed).

SPECIES	SAMPLE SIZE	SAMPLE DATE	MEAN INDIV-IDUAL WET WT.	MEAN INDIV-IDUAL DRY WT.	RATIO WET/DRY WEIGHT	MEAN-CALORIES PER GRAM WET WT.	MEAN CALORIES PER GRAM DRY WT.	MEAN INDIVIDUAL CALORIC CONTENT (Kilocalories)
Mallostus villosus (capelin)	12 (25)	July 1973	31.19	5.86	5.32	1004	5341	31.30
Hyas araneus (spider crab)	8 (6)	Jan. 1974	24.12	6.18	3.90	690	2691	16.63
Strongylocentrotus drobachiensis (sea urchin)	20 (6)	Jan. 1974	7.18	0.96	7.48	462	3458	3.32
Polynoidae (scale worms)	20 (2)	Jan. 1974	0.46	0.09	5.11	860	4396	0.40

Table 7. Caloric values for marine fauna of the North-west Atlantic.

SPECIES	CALORIC CONTENT	SOURCE
CLASS ECHINODERMATA		
Strongylocentrotus drobachiensis (sea urchin)	3448 cal/gm dry wt.	Reddin, (MSc./73).
" "	3458	Jenkins, present study.
" "	883	Brawn, et.al. 1968.
CLASS CRUSTACEA		
Meganyctiphanes norwegica (krill)	819 cal/gm wet wt.	
Mysis stenolepis (shrimp)	1029	
Pandalus montagui (shrimp)	1320	Tyler, 1971b.
Hyas araneus (spider crab)	945	
" " " "	348	Brawn, et.al. 1968.
" " " "	690	Jenkins, present study.
" " " "	2610 cal/gm dry wt.	Brawn, et.al. 1968.
" " " "	2691	Jenkins, present study.
Cancer irroratus (rock crab)	4211	Reddin, (MSc./73).
CLASS PISCES		
Mallotus villosus (capelin)	1004 cal/gm wet wt.	Jenkins, present study.
Tautogolabrus adspersus (cunner)	1058	Brawn, et.al. 1968.
Clupea harengus (herring)	1927	" "
" " "	2058	Tyler, 1971b.

then corrected for endothermy, whereas, the methodology used in this study and by Redding (1973) involved the removal of the test and determination of caloric values on dry weights of the contents only. This could account for these large differences in values; Brawn's et.al. (1968) being much lower because of the greater dry weight with the included test. Brawn et.al. (1968) also included the exoskeleton in the combustions of the spider crab. Their value of 2610 cal/gm dry wt. is quite similar to the value given in Table 6, 2691 cal/gm dry wt. The reactions involving the calcareous exoskeleton of the crab were corrected for. Tyler (1971b) on the other hand, found a much higher value for the spider crab, 945 calories per gram wet weight, compared to the converted wet weight value in Table 6, 690 cal/gm wet wt. Tyler removed the crab exoskeleton and this probably accounts for the higher caloric content, (very similar number of calories are present with and without the shell, but the number of calories expressed per weight decreases when the weight is increased with the presence of shell). It is also possible that apparent differences in caloric contents between workers might be accounted for on the basis of differences in the size of the animals sampled (Srivastava, 69/70 Bedford Biennial), or to seasonal differences in the caloric content of the organisms (Wissing and Hasler 1971). It is evident from Table 7 that capelin have a caloric value similar to that of the cunner, (1004 and 1058 cal/gm wet wt. respectively), but much lower

than the caloric content value for herring, (2058 cal/gm wet wt.).

The comparison of caloric values is difficult because there is no standard prodecure for the treatment of specimens for combustion. Some researchers include calcareous exoskeletons and correct for endothermy, while others remove the shell completely before combustion. Some express caloric contents in terms of wet weight and others use dry weights, or both. With no standard methodology, determining and comparing the significance of various prey organisms in a fish's diet is almost impossible. For this reason, mean individual caloric content values for each prey organism were determined, (see Table 6). This value was calculated using caloric measures expressed as either dry or wet weights, and represents the amount of energy available from one entire prey organism. If the entire prey is consumed, then this expression of caloric content is valid and useful for comparing different components of a predator's diet as relative sources of energy. From Table 6, it is apparent that capelin provide more energy per individual than do the other tested organisms. One capelin contains on the average 31.30 kilocalories, nearly twice that of one crab, and almost 100 times the energy in one scale worm. Table 8 illustrates the importance of each species in terms of wet weight and caloric content per individual. The Y/X value is a ratio expressing the number of organisms of species X required to equal the wet weight or caloric content of one organism of species Y. Hence, the mean

Table 8. Comparison of potential prey organisms showing their relative significance in terms of (a) mean individual wet weights and (b) mean individual caloric contents. Table values are Y/X ratios of the organism's respective weight or caloric value, (see text for explanation).

(a)

Y \ X	CAPELIN	CRAB	URCHIN	WORM
CAPELIN	1.00	1.29	4.34	67.22
CRAB		1.00	3.36	51.99
URCHIN			1.00	15.48
WORM				1.00

(b)

Y \ X	CAPELIN	CRAB	URCHIN	WORM
CAPELIN	1.00	1.88	9.43	78.25
CRAB		1.00	5.01	41.58
URCHIN			1.00	8.30
WORM				1.00

individual wet weight of capelin is 31.19 grams, and of a crab is 24.12 grams. The Y/X ratio (31.19/24.12) is 1.29, i.e. the wet weight of 1.29 intact crabs equal the wet weight of 1 capelin. It is evident from Table 8 that capelin provide the richest diet for the smallest individual weight of these prey organisms. Only 1.29 crabs are necessary to equal the wet weight of one capelin, but 1.88 crabs are required to provide the same amount of energy. This means that 0.59 (1.88 - 1.29), crabs or 14.00 grams of extra food weight is required to obtain the same amount of energy from a different prey organism. Similarily, 11.03 (78.25 - 67.22), scale worms or 5.07 grams of extra food weight are required for this prey. Not as much weight is necessary in the case of the scale worms because of their higher calorie per weight value. It is also because of this higher caloric content that fewer scale worms need to be consumed to equal the crab's caloric content than to equal the crab's wet weight, (i.e. 41.58 compared to 51.99).

Since capelin was the primary component of the longhorn's diet in early July 1973, the previously calculated daily ration can now be expressed as 10.2 grams of capelin per kilogram of sculpin. With the known caloric value for capelin, (see Table 6). the daily caloric ration or intake of the sculpin is 54.48 kilpcalories. Unfortunately, the individual prey weights were not determined during Tyler's (1971b) stomach analyses, and hence the daily ration in terms of prey weight

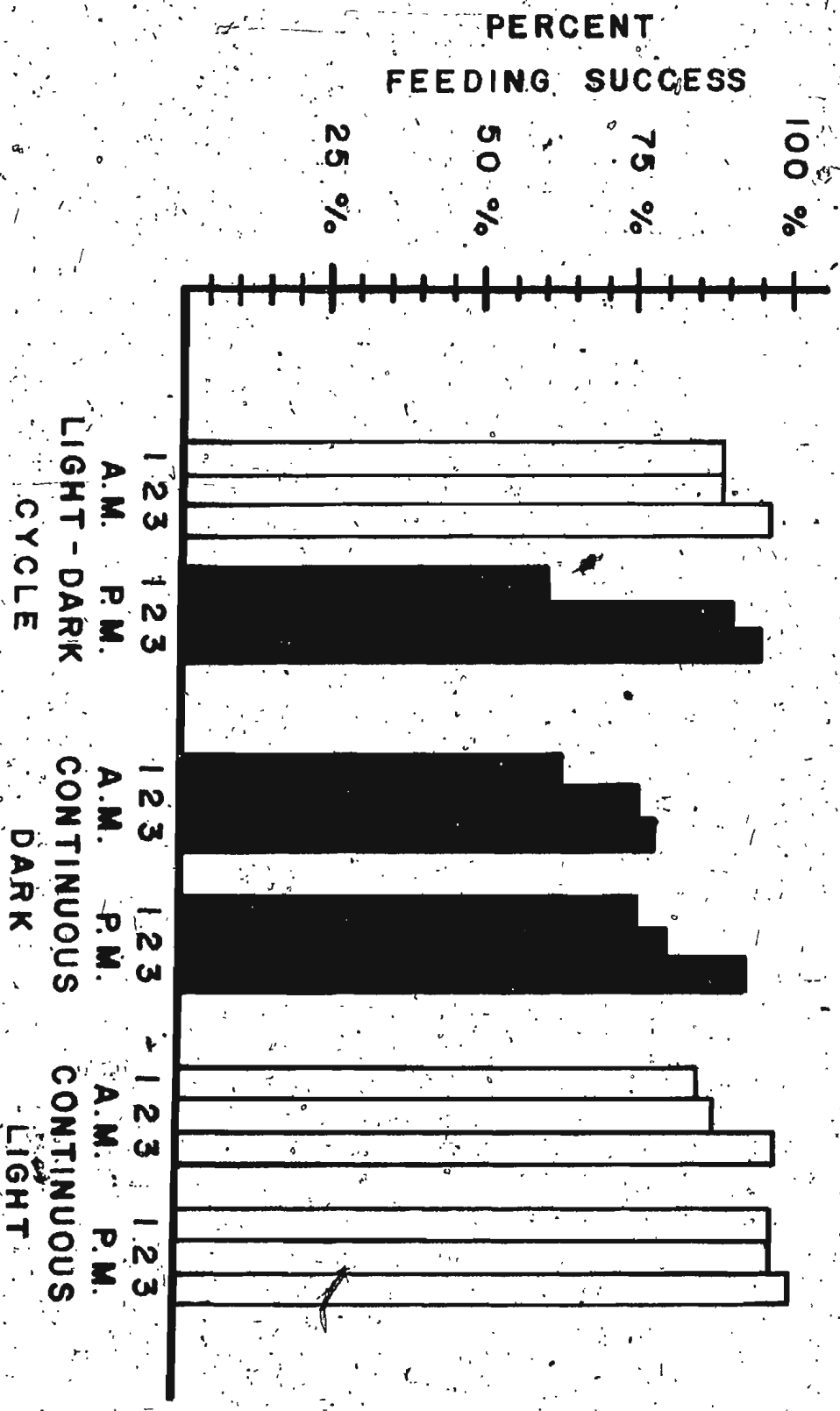
and calories can not be determined for the offshore sculpin populations, and no comparison can be made with the populations of longhorns found in shallower, inshore waters.

V. EFFECT OF LIGHT CONDITION ON FEEDING SUCCESS

Despite the wide temperature range which existed for the five independent feeding replicates, there was no sigificant difference in feeding success under identical light conditions between each replicate. An Analysis of Variance revealed a $P < 0.05$ for the calculated F values of each feeding exposure time.

The mean feeding success over the five replicates is given in Figure 11. It is apparent that feeding success is diminished under darkened conditions, although it still remained above 50 %. A Multivariate Analysis of Variance (Clyde 1969), was use to compare feeding success in relation to three independent variables; exposure time (1 minute, 10 minutes, and 2 hours), light condition (12 hour cycle, continuous light, and continuous dark), and feeding time (A.M. and P.M.). Two of these variables had a significant effect; both exposure time ($F = 5.581$, $P < 0.005$) and light condition ($F = 6.560$, $P < 0.002$), had a significant relation to the success of feeding. Feeding success is significantly higher under lighted conditions and is significantly increased with increased time of exposure to food. Thus, although conditions may not have been below the visual threshold of the sculpin

Figure 11. Results of the light/dark feeding experiment with the longhorn sculpin. Ordinate values are mean feeding success over five replicates, two fish per replicate. Success measured in relation to three independent variables; exposure time (1...1 min., 2...10 min., and 3...2 hours); feeding time (A.M. and P.M.), and light condition (12 hour light cycle, continuous dark, and continuous light). Darkened bars represent feeding under darkened conditions.


PERCENT
FEEDING SUCCESS
25 %
50 %
75 %
100 %
1 2 3 A.M. P.M. 1 2 3
LIGHT - DARK CYCLE
1 2 3 A.M. P.M. 1 2 3
CONTINUOUS DARK
1 2 3 A.M. P.M. 1 2 3
CONTINUOUS LIGHT

during the dark feeding conditions, a sufficient decrease in light intensity was achieved. This darkened light condition resulted in significant changes in feeding success, attesting to the importance of light for sculpin feeding.

DISCUSSION

In his review on the behaviour of littoral fish, Gibson (1969), states that methods of obtaining food are related to the kind of food ingested by the fish, and he concludes that feeding behaviour is basically the same for each feeding type. A comparison of the longhorn sculpin's feeding behaviour with other predators reveals a number of common patterns, and this suggests that Gibson's conclusion may not only apply to littoral fish, but to other marine and freshwater species as well.

The longhorn's locomotor behaviour characterized by numerous turns and excursions is one such common behaviour pattern. This swimming increases the amount of substrate the sculpin is exposed to and thus, increases the probability of an encounter with a prey organism. Olla, Samet, and Studholme (1972), describe a similar foraging behaviour which precedes feeding of the summer flounder (Paralichthys dentatus), and Olla, Wickland, and Wilk (1969), state that during feeding, the winter flounder (Pseudopleuronectes americanus), changes its direction and location every four to five minutes. That

few feeding responses were observed during the locomotor behaviour of the longhorn does not eliminate the possibility that this is an active searching behaviour. Barnett (1967), describes the appetitive component of feeding behaviour as being provoked by a bodily deficit, and that wide ranging movements within the environment of the organism are initiated by and maintained by specific internal states, even though evident reward in the way of food may be absent. The significant increase in locomotor behaviour of the experimentally starved sculpins suggests that these fish increased their food searching activities as a result of their food deprivation. Colgan (1973), developed a model where hunger was assumed to be jointly determined by metabolic need and gastric volume. On the basis of this model, he predicted behavioural changes of the pumpkinseed sunfish (Lepomis gibbosus), in the laboratory with changes in food deprivation. DeRuiter and Beukema (1963), found a decrease in the food searching activity of the stickleback (Gasterosteus aculeatus), with satiation and a corresponding rise in foraging behaviour with deprivation. It would seem on the basis of this evidence, that the locomotor behaviour of the longhorn could be a form of foraging. However, with no adequate controls in the field experiment, this cannot be conclusively demonstrated. The deprived experimental sculpins exhibited a directional offshore movement not observed for the non-experimental fish, suggesting that an avoidance response by the sculpins after long periods of captivity

may be influencing their locomotor behaviour. Although the exact nature of this locomotor behaviour has not been determined, the activity closely resembles the foraging behaviour of other marine and freshwater fishes, and the results from this study suggest that the sculpin's locomotor behaviour is a foraging activity.

The feeding behaviour of M. octodecemspinosus also has numerous action patterns which resemble those of other predators. The longhorn sculpin's feeding mechanisms most closely resemble those of the small marine cottid Parenophrys bubalis. Western (1969), describes P. bubalis as a visual predator of Crustacea (amphipods and crabs), which stalks its prey and attacks with a sudden forward lunge. Ingestion of smaller prey by "sucking" directly into the large terminal mouth and the forcing of larger prey down the esophagus by repeated "gulping" actions, are feeding characteristics common to both species. Olla et. al. (1972), describe similar visual fixation, stalk, and strike patterns for the summer flounder. The winter flounder expels mud, sand, and debris incidentally ingested, in an action comparable to that of the longhorn, (Olla et.al. 1969). Nursall (1973), describes ingestion by the freshwater perch (Perca flavescens), to be a kind of suction owing to a large rapid increase in the buccal cavity. This species of perch also exhibits a behaviour similar to the longhorn's socially facilitated feeding. One individual investigates a real or a potential prey and this activity attracts other perch, tending to reinforce the direction of the feeding

activity. One predatory perch rises to a prey and others follow, resulting in repeated feeding attacks. The group also chases prey along the bottom, the same feeding patterns observed when the longhorn sculpins respond to aggregates of cunner and also to released rock gunnels. Another freshwater predator with almost identical feeding actions is the northern pike (Esox lucius). Nursall's (1973) description of the pike's eye movements, orientation of the body axis towards the prey, stalk movements, followed by a quick lunge at the prey, closely resemble feeding actions of M. octodecemspinosus. The freshwater stickleback's complete response to prey discovery consists of fixating, grasping, and swallowing (DeRuiter and Beukema 1963); again, a striking similarity to the longhorn's actions.

There is definitely a stereotypy of predation behaviour among certain marine and freshwater predators. Although the behaviour may differ in small details, the feeding sequence does occur in a stereotyped pattern with similar basic characteristics.

The rooting behaviour observed at Outer Cove is similar to the chafe sequence of stickleback observed by Tugendhat (1960). The stickleback rotates its body to the side and with a strong tail beat, scrapes the gill cover against the hard surface of the aquaria. These chafes are often repeated several times in succession. This behaviour has not been observed in the field and no discussion of its functional significance was offered. The same kind of behaviour occurs in Blennius

pholis (blenny), Gadus morhua (cod), and Pleuronectes platessa (plaice), (Gibson, personal communication). Gibson (1968), describes this behaviour in the blenny as a displacement cleaning appearing in a conflict situation. He refers to the terminology of Wickler (1957), who describes this "cleaning behaviour" in the two blennies B. fluviatilis and B. pavo. The rooting behaviour of the longhorn sculpin could be this cleaning behaviour. The abrasive action of the sand may be used to remove irritating ecto-parasites. For this to be the case however, it would have to be demonstrated that, (1.) sculpins can sense the presence of ecto-parasites and (2) these parasites are irritating to the fish. This would be a difficult task. Furthermore, the rooting has been observed elicited by individuals with no obvious ecto-parasites and longhorns heavily infested with parasites in laboratory aquaria do not exhibit rooting behaviour. Further observations are necessary before this behaviour can be conclusively termed "cleaning behaviour".

There is a second thesis that can explain the function of this behaviour. The rooting could disturb and expose food organisms such as small Crustacea or Annelida from the sand. These organisms occur in longhorn stomachs and such behaviour would be advantageous to the foraging sculpin. Although initial observations indicated this might be the case, (hence the term rooting), further observations suggest this might not be true. The sculpin does not return to the disturbed region after a rooting series and feeding does not occur during the

actual behaviour. Only one feeding response was observed after a rooting series and this occurred about one metre beyond the disturbed region. If food organisms are exposed by this behaviour, the sculpins do not appear to feed upon them.

Light plays a dominant role in the perception of food by the longhorn sculpin, and accordingly, this predator can be termed a "visual predator", (see Blaxter 1970, for a discussion of this term). Direct observations of visual fixation upon prey in the laboratory and in the natural environment provide evidence that light is required or at least used by the longhorn sculpin. Behavioural observations as a criterion used to determine the importance of light to feeding fish were used by Marak (1960). The second criterion for visual feeding by the longhorn sculpin is the more exact information available from the light/dark laboratory feeding experiments, i.e. feeding is significantly reduced under conditions of darkness. The most striking feature arising from these experiments however, is that the longhorn sculpin has the ability to feed quite successfully under dark conditions. This suggests that vision is an important sensory mode for food detection, but it is not essential for successful ingestion. Blaxter (1968), found similar laboratory results with young plaice (Pleuronectes platessa), feeding upon live Artemia nauplii. He suggested that another sense, either chemical or mechanical, is operating. The response of the sculpins to the PVC feeding cylinder which masked

visual perception of the food, indicates sculpins also have the ability to detect the presence of food by other sensory modes. M. octodecemspinosus, like the cod (G. morhua, Brawn 1969), relies heavily upon vision to locate food, but switches search modes under extreme feeding conditions. These secondary modes however, are not as efficient as the primary visual perception.

These laboratory results indicate that the longhorn sculpin has the sensory and behavioural ability to feed under dark conditions. However, feeding by night under tank conditions is not necessarily evidence of nocturnal feeding in the natural environment. Hoar (1942), discovered a learning factor which affected feeding success of Salmo salar on chopped earthworm. Blaxter (1968), also found residual feeding in dark laboratory experiments, and suggested that learning and type of food may affect feeding behaviour. The longhorns were confined in small paritioned areas, but it is unlikely that two trial learning over a period of 12 hours could occur, and even if it did, retention of such a learning factor over a two week starvation period between replicates is even more unlikely. The small feeding space did restrict the locomotor activity of the sculpins, and as a result, feeding success was measured only under conditions where food was in the immediate vicinity of the sculpin. However, such conditions can and do exist in the natural habitat. Rifts of dead capelin are regions of sculpin aggregations and stomach content analysis revealed successful

ingestion of dead capelin during all hours of the 24 hour day. Quite clearly, a longhorn situated on a capelin rift has the ability to successfully feed upon this food resource. As sculpins were observed to be inefficient predators of live fishes like the rock gunnel, during the day, it is not likely that this species of sculpin is an effective predator of small benthic fishes during periods of darkness.

Methods of determining changes in the feeding intensity of fish in the natural environment in a given 24 hour period have been discussed by Surber (1930) and Darnell and Meierotto (1962), and have recently been employed by numerous other workers. The most common approach is to infer feeding times from the weight of stomach contents sampled over a 24 hour period, (Seaburg and Moyle 1964, Keast 1968, and Keast and Welsh 1968). Edwards and Steele (1968), and Gibson (1973), used a modification of this method. They sampled stomachs over the daylight hours, then performed a multiple regression of the data searching for significant changes in stomach content weight as the day progressed. Kruuk (1963), used intestinal contents as an index of feeding periodicity in the common sole (Solea vulgaris). The percentage of soles with food in the intestinal tract and food position in the intestines were determined and statistically analyzed with a X^2 test. A third index of feeding periodicity, used for comparison with and verification of stomach content weights, is the occurrence of various stages of digestion in the stomach. Darnell and Meierotto (1962),

Mathur and Robbins (1971), and Mathur (1973), found a correspondence between stomach content conditon and peak times of stomach content weight.

The validity of some of these applications of the 24 hour sampling technique to infer feeding periodicity is now under question. With the exception of Kruuk (1963), Edwards and Steele (1968), and Gibson (1973), no statistical analysis of this kind of data has been published. Yet, definite feeding periodicities have been inferred from data characterized by large scatter about mean values. The data presented for the longhorn sculpin stresses the importance of applying rigorous statistical analysis to 24 hour sampling data and of accounting for the large amount of variability, before concluding the presence of cyclic feeding. Definite cyclic feeding trends were suggested by the three most common measures of feeding periodicity, and yet no conclusions about cyclic feeding in the longhorn sculpin can be made because of the results of the statistical tests. Time did not have a significant effect upon these three measures and only a small proportion of the large variability present in the data was accounted for by time of sampling. Feeding intensity is not only affected by prey distribution, prey size, availability of prey, and predator size (Ivlev 1961), but variations in movements, experiences, and motivational levels of the predator also influence the rate at which they consume food, (Ware 1971).

At the individual level, a complex array of biotic and abiotic factors affect ingestion rates, and this accounts for the large degree of variation in stomach content data. Cyclic feeding is only one cause of the observed scatter, and its accurate determination is not possible without a consideration of the other causes of individual variation in stomach contents.

M. octodecemspinosus then, is not a cyclic feeder during the capelin spawning period at least. It has the physical and behavioural ability to successfully ingest certain kinds of food under night conditions and the field studies indicate that food consumption does in fact occur throughout the 24 hour period.

BEHAVIOURAL ECOLOGY OF THE LONGHORN SCULPIN

Tyler (1971a), classifies M. octodecemspinosus as a regular component of the demersal fish community of Passamaquoddy Bay, N.B. on the basis of its continued presence during seasonal trawls. Fluctuations in abundance of this species still occurred however, with times of decreasing numbers offshore corresponding to the establishment of summer inshore populations. In Newfoundland, longhorns move inshore about mid-May and remain in these shallow waters till the end of September, (Pepper, personal communication). Tyler (1971b), also found pronounced differences in the quantity of food in the stomachs of longhorn sculpins for different months, and he suggests that these fluctuations are caused by the absence of principal prey (see Tyler 1972,

re this term), in the stomach. Some of the months of decreased stomach content weight appear to correspond to times of onshore movement, and it is possible that these onshore movements are a summer phenomenon related to feeding. Bigelow and Welsh (1925), state that the seasonal migrations of the longhorn in the Bay of Fundy region are related to temperature. Morrow (1952) however, concludes that temperature is not the controlling factor, but may only contribute to these seasonal migrations. Morrow also determined monthly changes in the coefficient of condition of the longhorn sculpin, and times of weight loss correspond not only to breeding times, but also are coincident with the onshore movements of this species. If such changes in weight accompany these onshore movements, then there must be a sufficient food resource inshore to sustain the population during the summer. In Newfoundland waters, the spawning capelin provide just such a resource. During this spawning period, an unlimited food resource is established under conditions of no competition, and sculpins need not be terribly efficient to obtain large rations of this rich food source. Feeding can occur at all hours of the 24 hour day and the longhorns literally engorge themselves on this one food. The capelin provide the richest diet for inshore populations of the longhorn sculpin. This is not only in terms of energy content of the prey, but also with regard to the amount of energy expended to capture

and ingest the prey. Ingestion of capelin during their spawning period requires no foraging or pursuit, as this food is ingested dead from the rifts of capelin bodies left after the spawn. More energy would be expended in the search for and capture of crabs and even more to encounter and ingest worms, for a smaller return in energy. A minimum of energy expenditure through foraging behaviour, concurrent with an inexhaustable food supply rich in calories, provides an ideal situation for increasing the growth of individual longhorns. Offshore populations of the longhorn ingest primarily the krill (Meganyctiphanes norwegica) during the summer, (Tyler 1971b), which has a substantially lower caloric content than the principle prey of the longhorn inshore, i.e. the capelin, (see Table 7). Offshore populations of the longhorn sculpin ingest primarily Mysis stenolepis and Pandalus montagui; a crustacean diet rich in energy (comparable to and exceeding the capelin, see Table 7), although most probably more costly in terms of energy to obtain. It is suggested that the large scale movements of M. octodecemspinosus to shallower inshore regions during the early summer, may in fact be a phenomenon related to the availability of large amounts of this energy rich food.

During the interval preceding the capelin spawning period and for a short period thereafter, smaller benthic fishes like the diurnally active rock gunnel and the nocturnal radiated shanny, are potential prey

for the longhorn. The sculpin's feeding behaviour seems suited for successful utilization of these fishes. The longhorn lies in wait for extended periods and quickly lunges to ingest its prey, and also makes forays about its territory, apparently in search of food. However, longhorns are not effective predators of these fish. The sculpin does repond to these smaller benthic fishes, but is not successful in its ingestion attempts. Nursall (1973), observed similar inefficient predation attempts by the freshwater northern pike, and states that the abundance of the prey fish probably compensates for the low predation success rate. The rock gunnel and radiated shanny however, are not in great enough abundance to compensate for the ineffective longhorn, and therefore, do not appear to be an important food resource for this species of sculpin.

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APPENDIX I. Individual Quantitative Data of the Swimming Activity of Non - experimental *Myoxocephalus octodecemspinosus*.

DATE 1973	TIME	LOCATION	EXCURSIONS PER MINUTE	TURNS PER MINUTE
July 30	1400	Outer Cove	0.00	0.00
July 30	1400	" "	0.65	0.00
Aug. 1	1400	" "	0.30	0.18
Aug. 2	1330	" "	0.07	0.06
Aug. 2	1500	" "	0.05	0.02
Aug. 2	1500	" "	0.00	0.08
Aug. 25	1700	" "	0.07	0.07
Aug. 26	1730	" "	0.07	0.03
Aug. 26	0800	" "	0.16	0.13
Aug. 26	0900	" "	0.22	0.24
Sept. 13	1000	" "	0.08	0.05
Sept. 13	1100	" "	0.13	0.13
Sept. 13	1130	" "	0.07	0.07
Sept. 14	0700	" "	0.10	0.10
Sept. 15	0700	" "	0.00	0.00
Aug. 20	1300	St. Phillips	0.26	0.22
Aug. 22	1900	" "	0.08	0.12
Aug. 27	1500	" "	0.00	0.00
Sept. 13	1600	" "	0.43	0.47
Sept. 20	1600	" "	0.00	0.07
Sept. 24	1400	" "	0.70	0.76
Aug. 22	0800	" "	1.05	1.05
Aug. 24	1030	" "	0.00	0.03
Sept. 18	1000	" "	0.00	0.00

APPENDIX 2. Individual Quantitative Data of the Swimming Activity of Experimental and Control M. octodecemspinosus at St. Phillips. (C designates controls, i.e. starved then fed).

DATE 1973	TIME	NUMBER OF DAYS STARVED	EXCURSIONS PER MINUTE	TURNS PER MINUTE
Aug. 6	1430	11	0.14	0.32
Aug. 6	1500	11	1.32	1.08
Aug. 8	1900	13	0.33	0.33
Aug. 9	1400	14	1.11	1.02
Aug. 13	1230	18	0.57	1.43
Aug. 14	1900	19	0.39	0.45
Aug. 16	1200	21	0.47	0.66
Sept. 11	1500	C 14	0.90	0.50
Sept. 11	1530	C 14	0.09	0.03

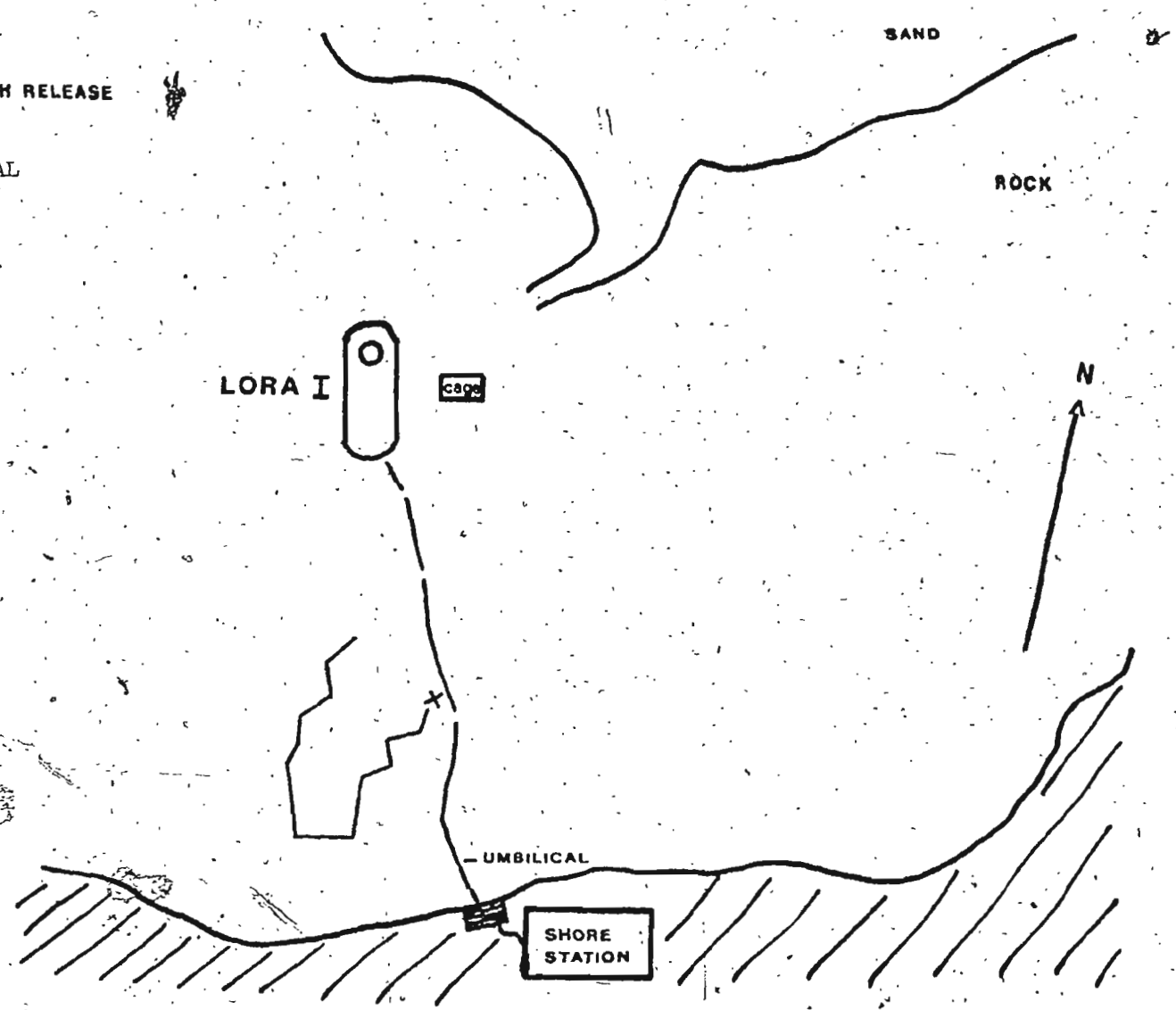
APPENDIX 3. Relative Mappings of the Locomotor Behaviour of Non-experimental and Experimental M. octodecemspinosus.

ST. PHILLIPS

X = SITE OF FISH RELEASE

NON-EXPERIMENTAL

20 / 8 / 73

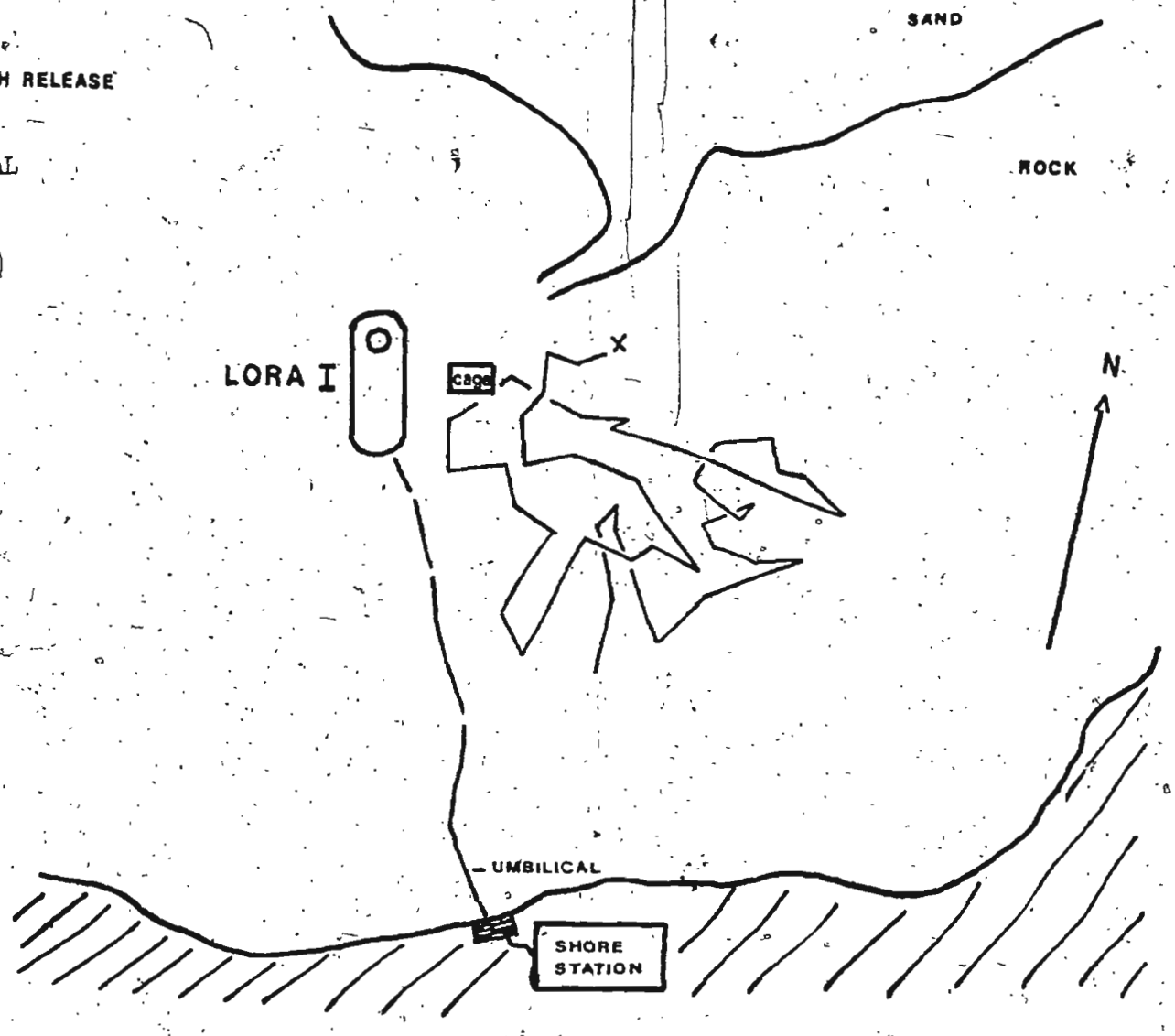


ST. PHILLIPS

X = SITE OF FISH RELEASE

NON-EXPERIMENTAL

22 / 8 / 73

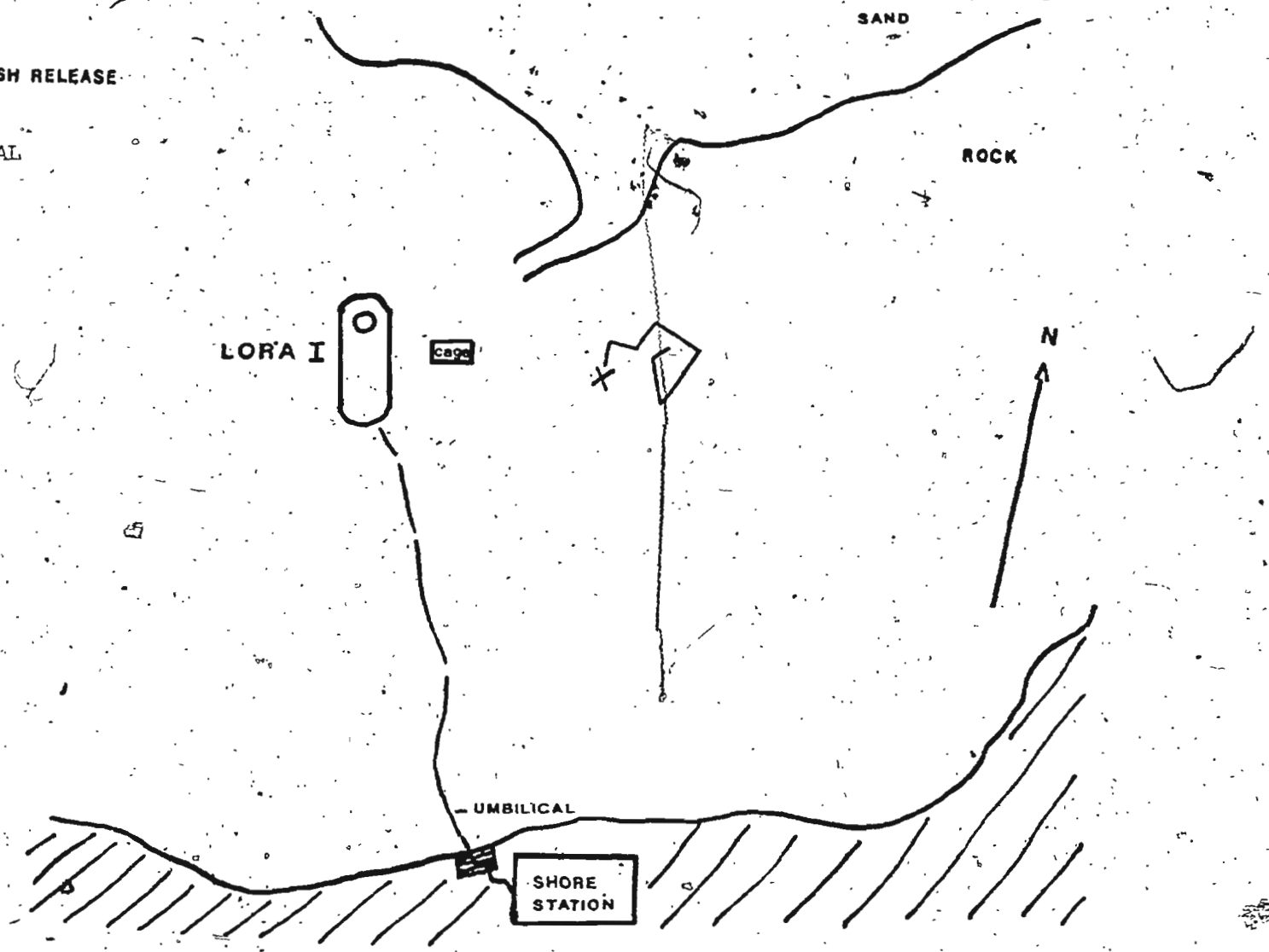


ST. PHILLIPS

X = SITE OF FISH RELEASE

NON-EXPERIMENTAL

22 / 8 / 73



ST. PHILLIPS

X = SITE OF FISH RELEASE

NON-EXPERIMENTAL

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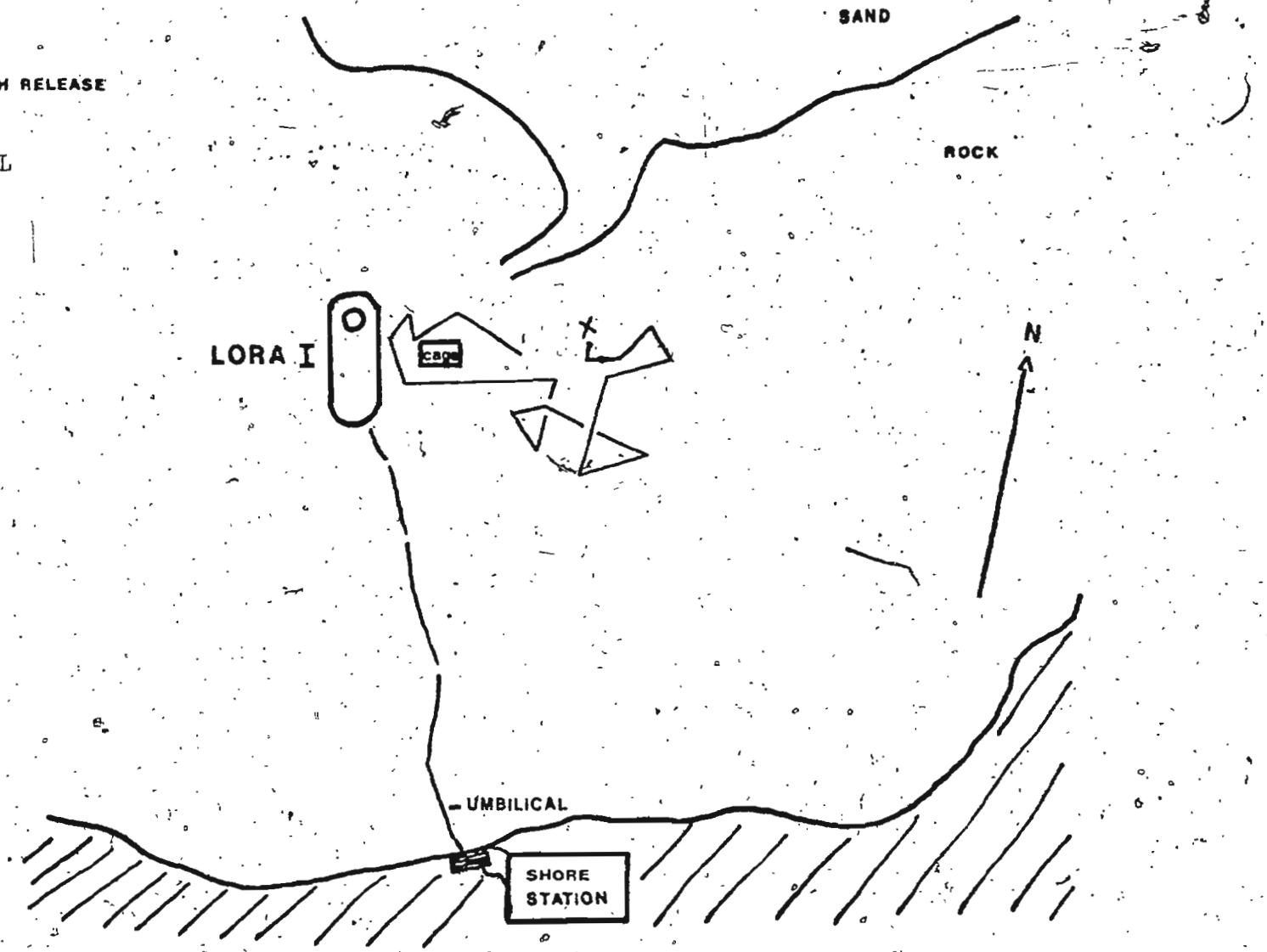

ST. PHILLIPS

X = SITE OF FISH RELEASE

NON-EXPERIMENTAL

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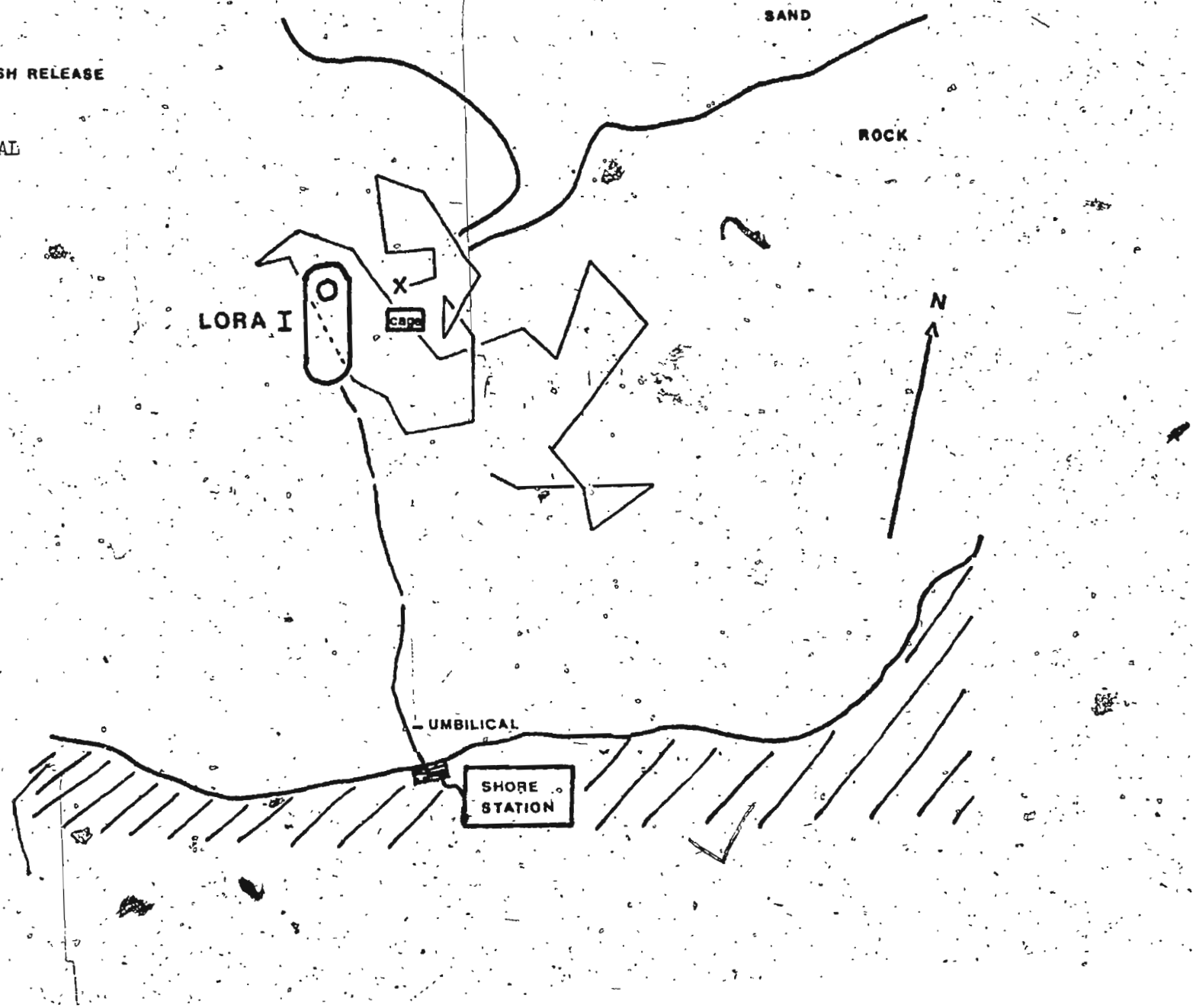


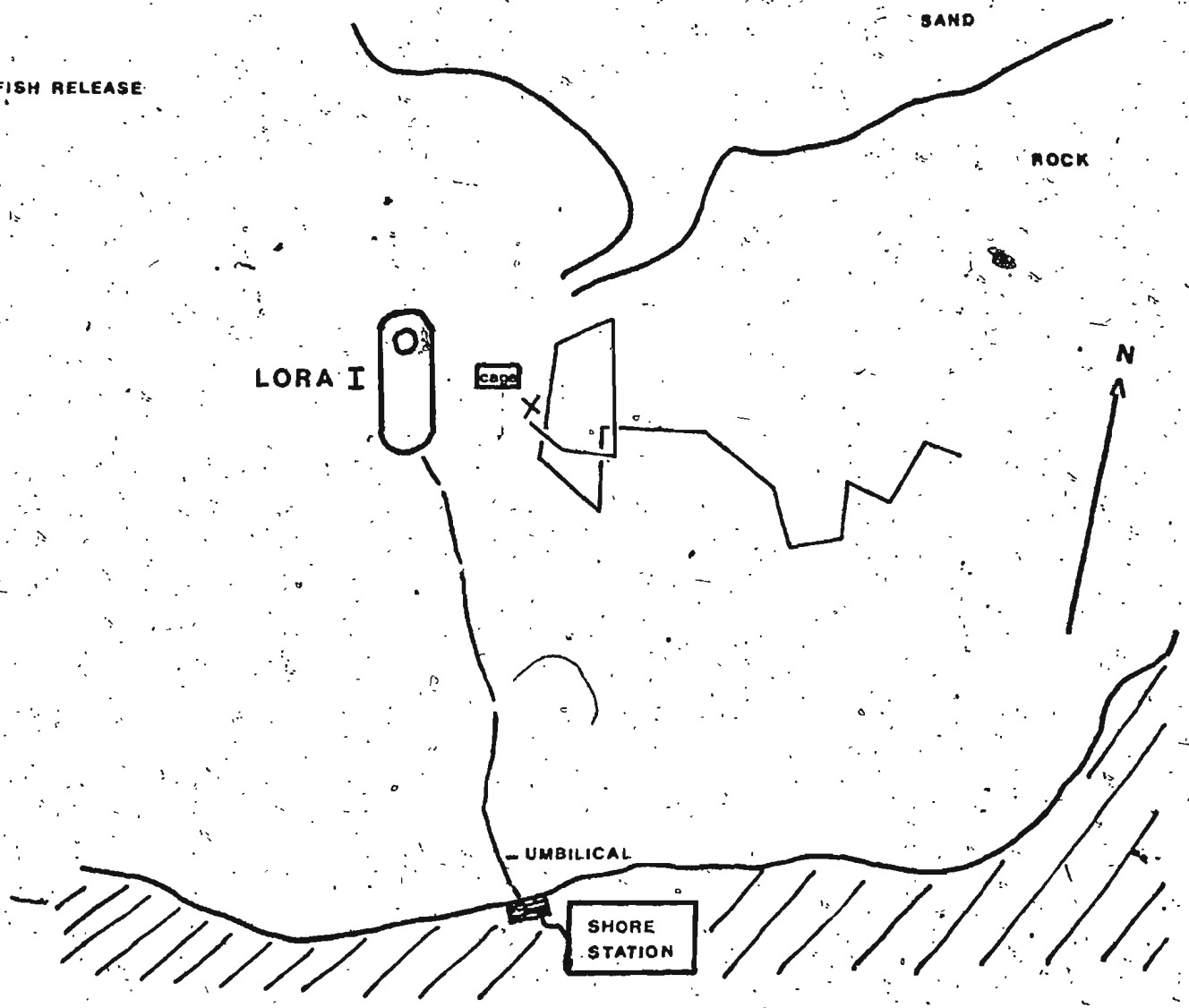
ST. PHILLIPS

X = SITE OF FISH RELEASE

EXPERIMENTAL

6 / 8 / 73

FISH # C



ST. PHILLIPS

X = SITE OF FISH RELEASE

EXPERIMENTAL

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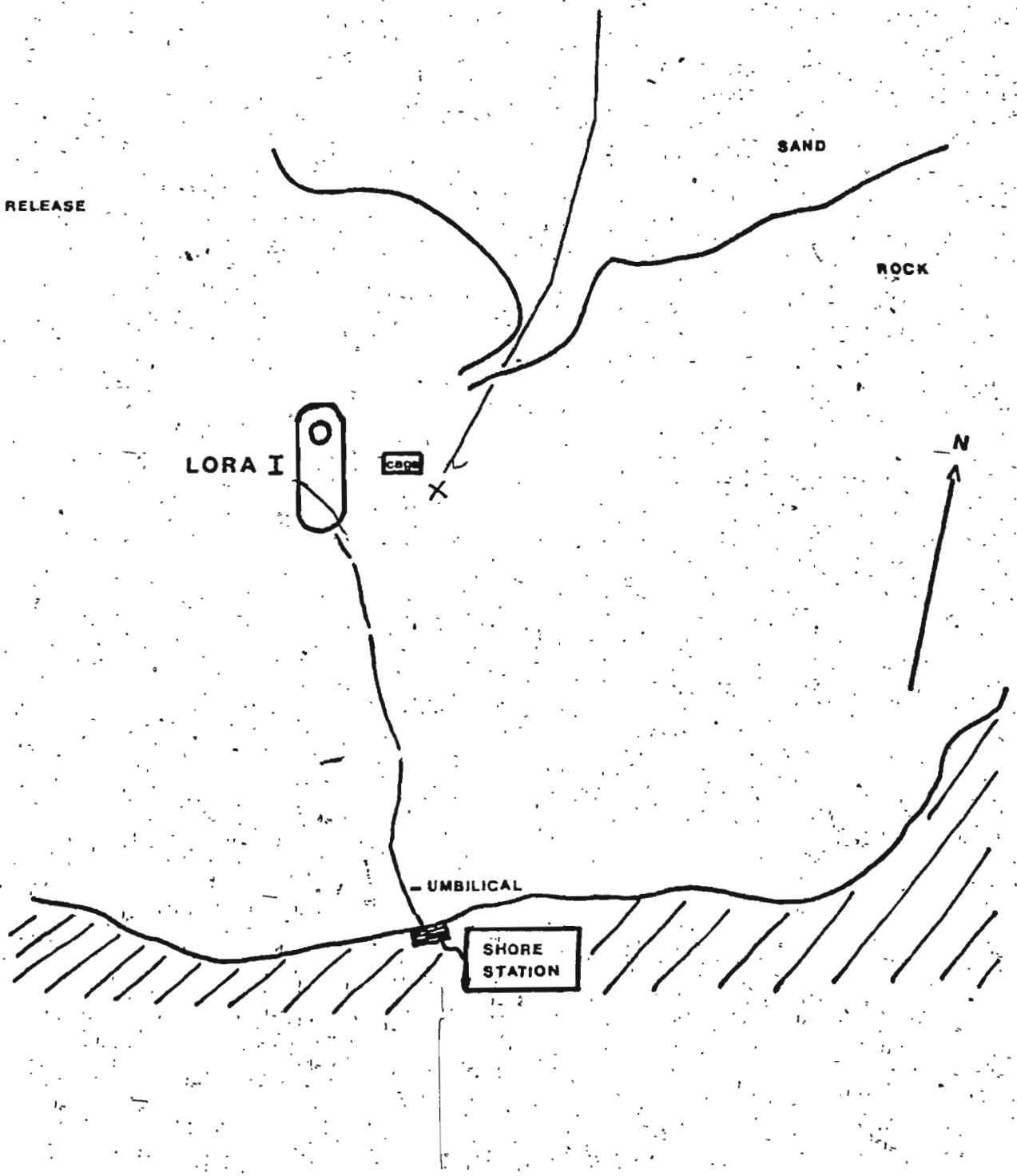

ST. PHILLIPS

X = SITE OF FISH RELEASE

EXPERIMENTAL

9 / 8 / 73

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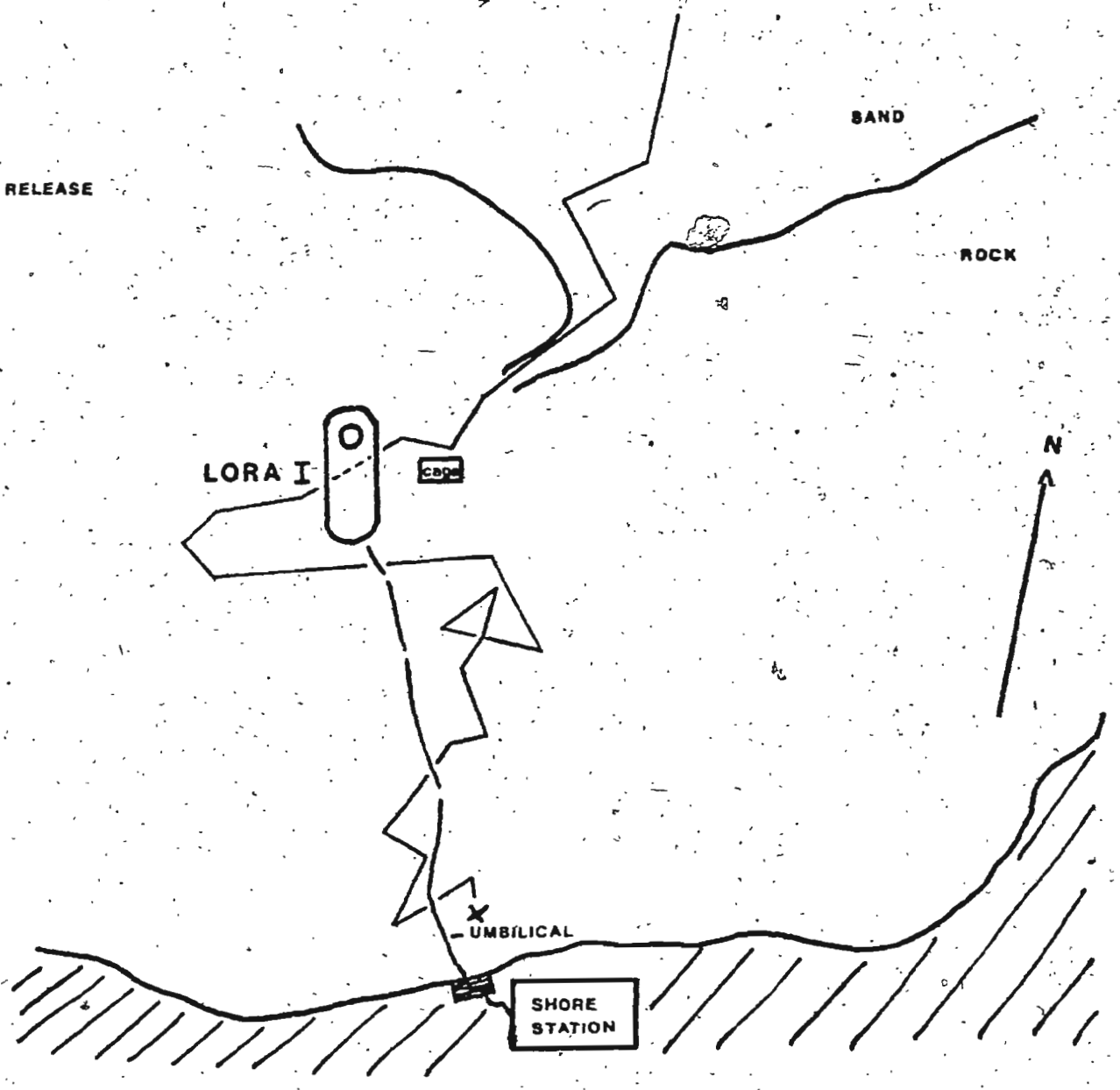


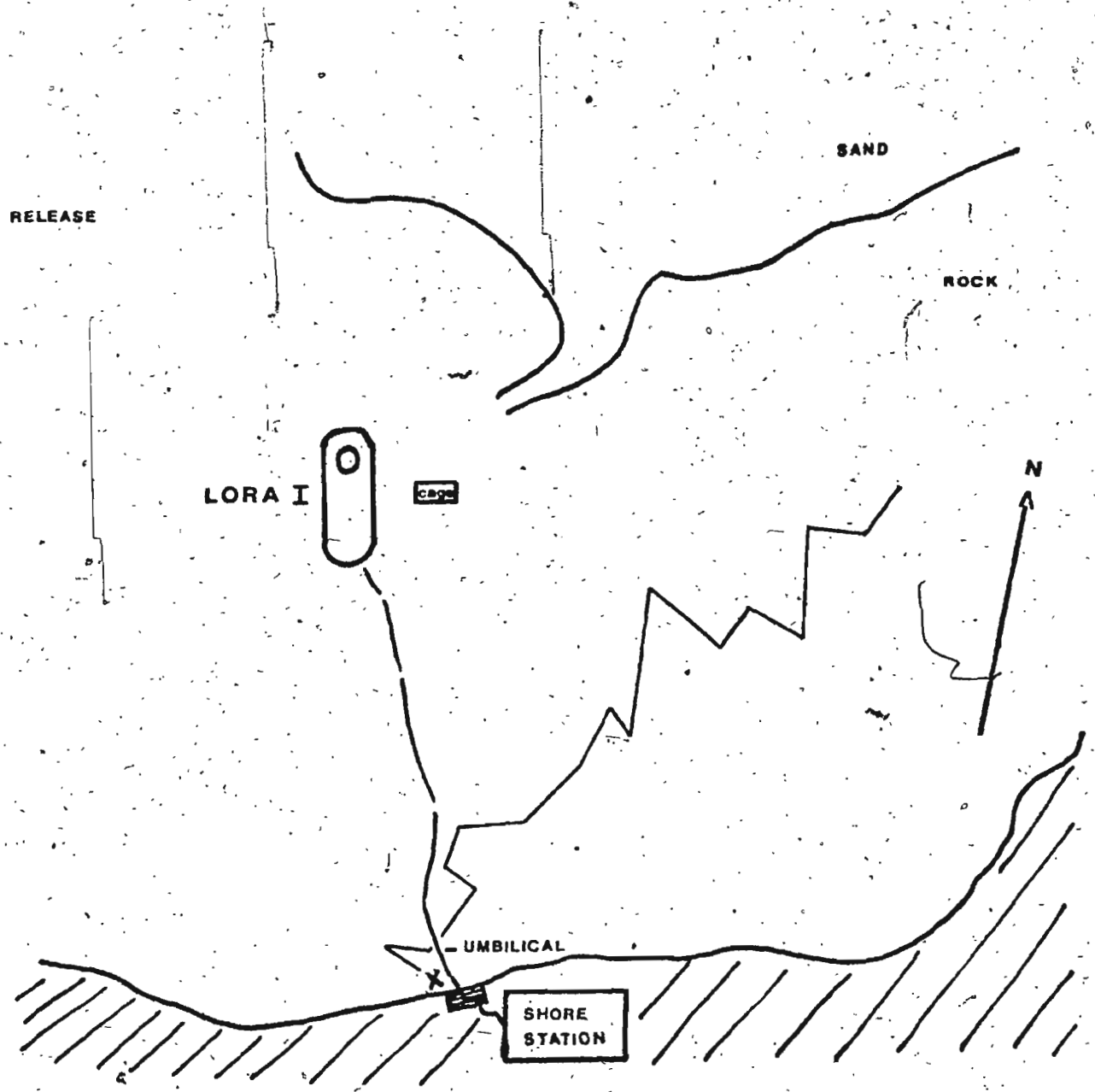
ST. PHILLIPS

X = SITE OF FISH RELEASE

EXPERIMENTAL

13 / 8 / 73

FISH # B.



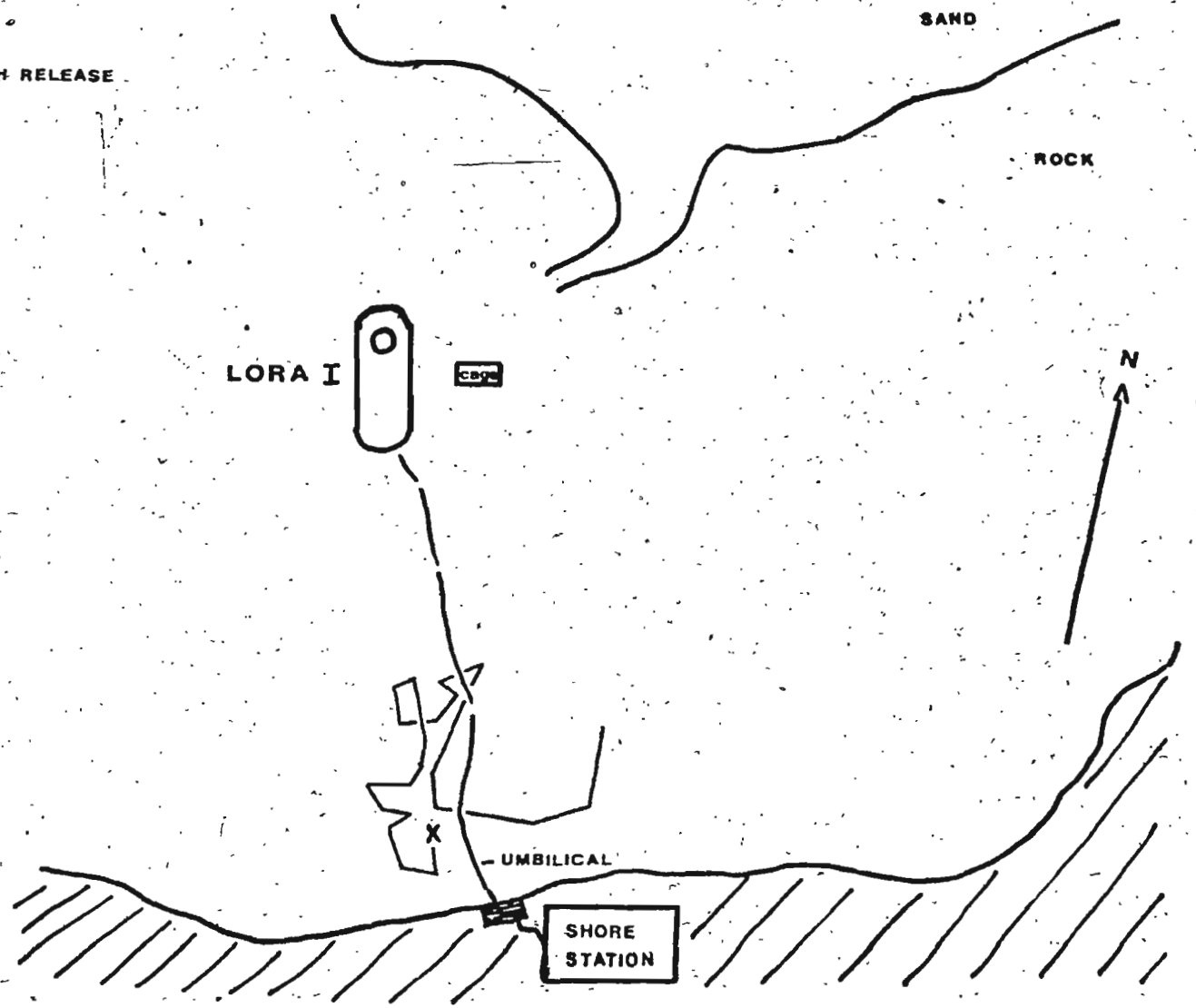
ST. PHILLIPS

X = SITE OF FISH RELEASE

EXPERIMENTAL

14 / 8 / 73

FISH # F



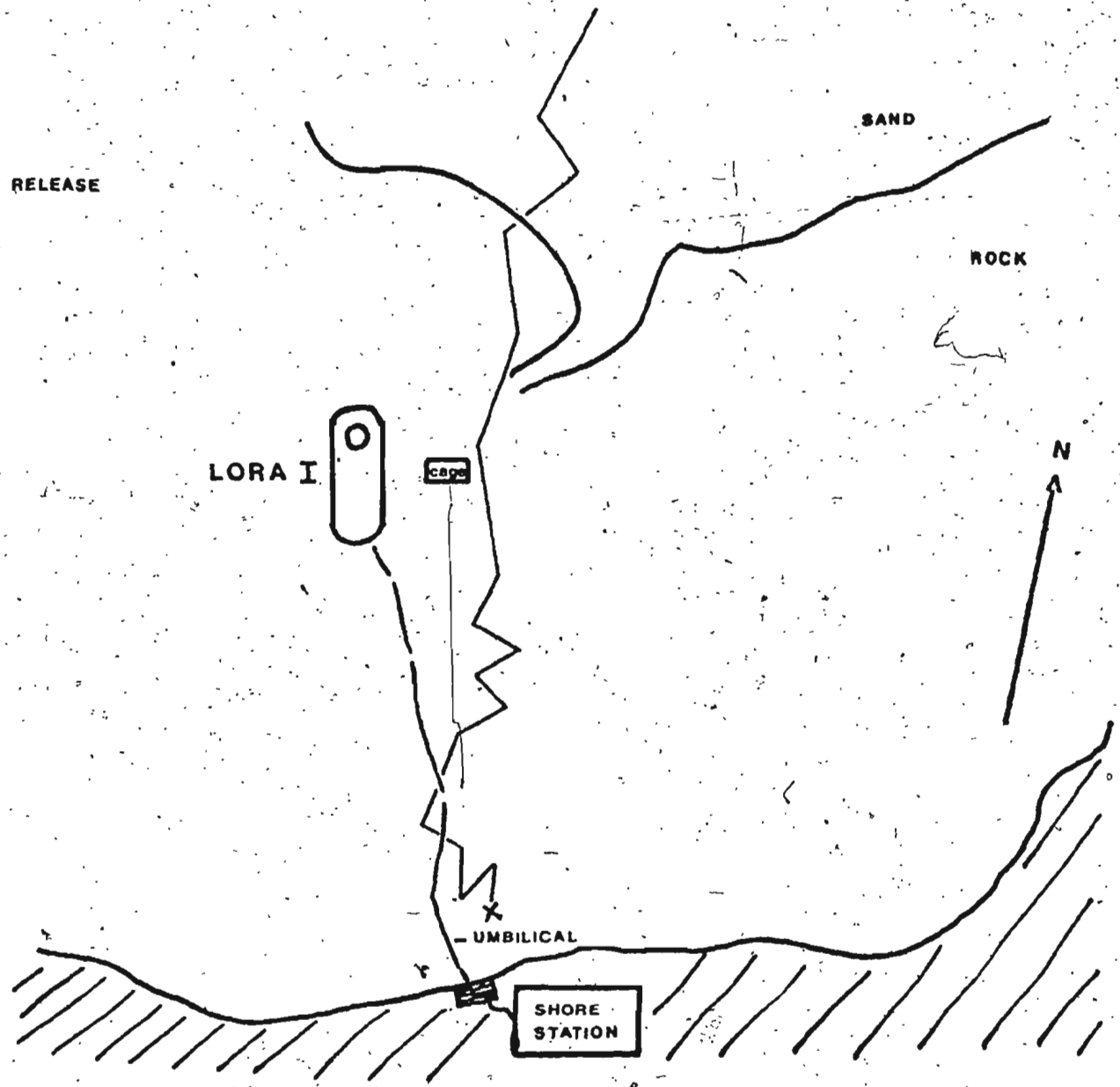
ST. PHILLIPS

X = SITE OF FISH RELEASE

EXPERIMENTAL

16 / 8 / 73

FISH # E



ST. PHILLIPS

X = SITE OF FISH RELEASE

EXPERIMENTAL - CONTROL

11 / 9 / 73

FISH # 00866